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A NEW MIOCENE RODENT FROM EAST AFRICA

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A NEW MIOCENE RODENT FROM EAST AFRICA

By D. G. MacInnes

INTRODUCTION

The material described in this paper was collected from the Miocene sediments of Songhor and Rusinga Island in Kenya Colony. The work was financed by grants from the Kenya Government, and by generous donations from C. W. Boise, Esq.

A new genus and subfamily of the Pedetidae is described. The first examples to be found included some fragments of mandibles and limbs collected on Rusinga Island in 1932, but it was not until 1948 that a relatively complete specimen was obtained. This was found in the Songhor deposits, and has been made the type-species of the genus. Fragments of another skeleton from Wanyama (Lower Hiwegi series), on Rusinga Island, are included among the paratypes of the species.

An interesting feature of the genus is that it still retains a fully developed hallux, besides showing certain other anatomical details which may be taken to indicate a less highly specialised animal than the Recent *Pedetes*. In the genus *Parapedetes* Stromer, although of approximately the same age as the new specimens, the hallux was already suppressed, and it appears to have been even more specialised than the Recent genus in several other features. No examples of *Parapedetes* have yet been found in the Kenya Miocene deposits.

In the Recent *Pedetes* the proportion of skull to head-and-body length is about 22%. The skull of the fossil measures 119 mm., suggesting that the head-and-body length was 540 mm., compared with about 400 mm. in the modern animal.

The material will be divided between the British Museum (Natural History), and the Coryndon Museum, Nairobi.

Family PEDETIDAE Owen 1847

Sub-family MEGAPEDETINAE subfam. nov.

Diagnosis.—Medium to large pedetids in which the cheek-teeth were of limited growth. Fibula reduced, but not necessarily fused with tibia. No reduction of digits in manus or pes.

MEGAPEDETES gen. nov.

Diagnosis.—A large pedetid in which the cheek-teeth were of limited growth, each with a median transverse fold not extending throughout the whole vertical height of the crown ; hind foot with fully developed hallux.

Type Species.—*Megapedetes pentadactylus* sp. nov.

Megapedetes pentadactylus sp. nov.

Diagnosis.—As for the genus.

Holotype.—The greater part of a skeleton, including a slightly damaged skull and mandible with complete dentition except for M^3 : most of the axial skeleton : the main bones of both front and hind limbs, and a large part of the right manus and the left pes (No. Sgr. 420. '48).

Horizon.—Lower Miocene.

Locality.—Songhor, Kenya Colony; Lat.: 0°23'S: Long. 35°14'E.

Material.—From Songhor, the holotype, and 16 other fragments, including two halves of a single mandible, found in 1948 and 1949 respectively. From Wanyama, Rusinga Island, a crushed fragment of skull-cap, mandible and lower dentition, with associated cervical vertebrae, scapula and long bones of both front limbs (No. 982, '47). From other sites on Rusinga Island, two fragments of femur, a right astragalus and a right and left metatarsus (R.1932) : 4 maxillary and mandibular fragments with lower dentition complete (366.'48) : a mandibular symphysis (759.'49) : 2 isolated astragali (490.'48 and 291.'49) : some 40 incisor fragments and 20 isolated cheek-teeth.

An analysis of the sites from which the material was obtained is as follows :—

Kathwanga series	1%
Hiwegi series	86%
Kiahera series	13%

In view of the relative scarcity of specimens of this genus, the significance of these figures is doubtful.

The Skull

The anterior part of the Songhor skull is complete, and also most of the left side. The whole of the right parietal region and most of the basi-cranium is missing. In the left profile (Plate I, fig. 1 ; Text-fig. 1) the general superficial resemblance to the skull of *Pedetes* is very striking. Fuller examination shows, however, that there is little similarity of detail. The following description is based largely upon the more complete skull of the holotype (Sgr. 420.'48) ; for comparison an adult skull and skeleton of *Pedetes surdaster larvalis* Hollister is used throughout. The latter is about three-quarters of the size of the fossil. A diagrammatic restoration of the skull and mandible is shown in Text-fig. 1.

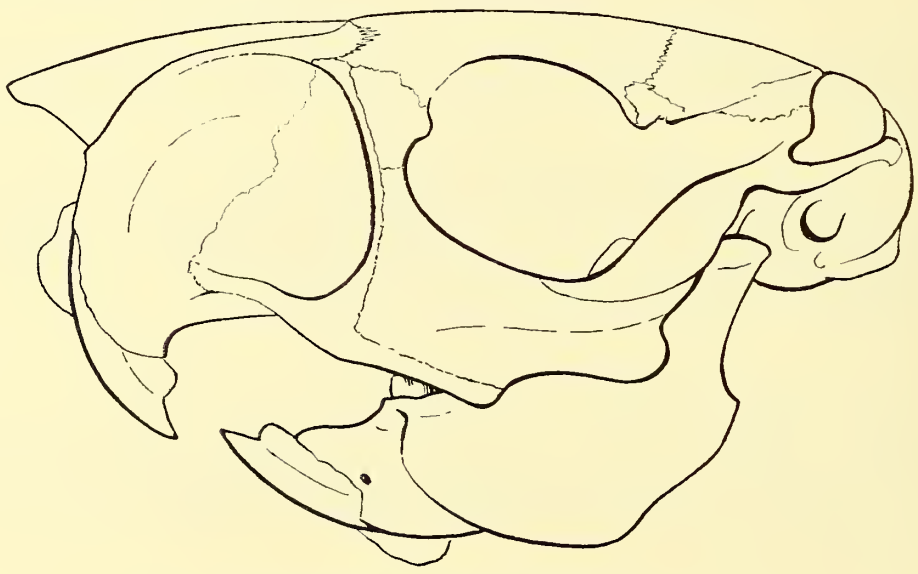

Fig. 1. *Megapedetes pentadactylus* : Restoration. ×$\frac{1}{2}$.

Dorsal surface. (Text-fig. 2).—The nasal bones are long (47·0 mm.) and relatively narrow, with the maximum breadth (17·0 mm.) across the anterior part. The minimum width, at about the middle of their total length, is 14·0 mm., and thereafter the breadth increases again gradually to 16·0 mm. at the posterior end. In *Pedetes*, although the maximum length of the nasals is only 28·0 mm., the breadth is 20·0 mm. near the middle, and the bones taper to 19·0 mm. posteriorly and 16·0 mm. anteriorly. The middle part is more inflated and the anterior part more depressed in *Pedetes*, whereas in the fossil the upper surface is nearly flat. The upper extensions of the pre-maxillae overlap the sides of the nasals, and have a faint ridge separating the dorsal surface from the lateral walls. From a point about 9 mm. in front of the naso-frontal suture these ridges turn outwards and downwards in a smooth curve, to unite with the pre-orbital processes of the maxillae and form the postero-external border of the infra-orbital foramen. In *Pedetes* the upper part of the pre-maxilla does not overlap the nasal, but forms a thin plate bounded dorsally by a very sharp ridge overhanging the lateral wall of the muzzle. The two ridges are parallel to one another until just behind the naso-frontal suture, where they turn sharply outwards and downwards, almost at right-angles to the long axis of the skull.

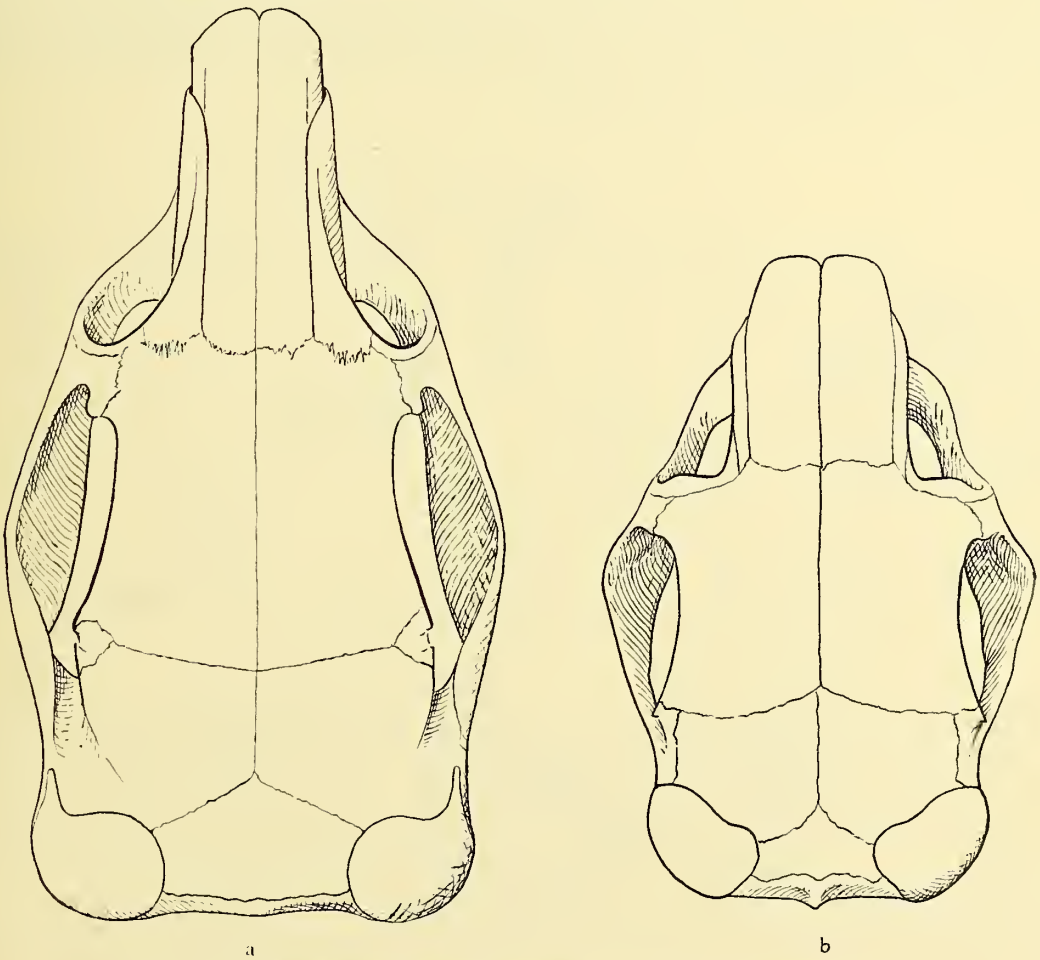

Fig. 2. (*a*) *Megapedetes* (partly restored). × 1. (*b*) *Pedetes*. × 1.

The frontals are considerably narrower in the fossil than in *Pedetes*, and whereas in the latter the upper rims of the orbits are parallel, in *Megapedetes* they diverge towards the back. The depression normally present in the region of the anterior half of the frontal suture in *Pedetes*, was evidently very pronounced as a wide median groove, but unfortunately the posterior edges of both the frontals and almost the whole of both parietals are crushed or missing. The fronto-parietal suture lies at the level of the posterior edge of the orbit, as in *Pedetes*. The posterior dorsal rim of the orbit is extended downwards and outwards by a small post-orbital process of the squamosal, and the fronto-parieto-squamous junction lies on the dorsal surface slightly to the median side of the process. The inter-parietal appears to have been similar to that of *Pedetes*, and the posterior lateral corners of the skull are formed by large rounded extensions of the supra-tympanic. Although the posterior part of the cranium is severely damaged there is no indication of the median upward inflation of the fronto-parietal region of *Pedetes*, or of the depression of the hind part of the parietals and inter-parietal. The dorsal surface of the skull is thus flatter in the fossil. This condition is also found in the cranial fragment from Rusinga, which represents a slightly larger individual. Almost the whole of the zygomatic arch, and the greater part of the mastoid region of the left side are preserved in both examples, as well as much of the middle line, and it is thus possible to make a comparatively accurate estimate of the total breadth of the skull at various points. The measurements of the dorsal surface, in millimetres, are as follows :—

	Megapedetes		*Pedetes*	Proportion
	Holotype	982.'47		
Maximum length . . .	119	—	86	138%
Muzzel breadth	21·5	—	23	93%
Inter-orbital breadth . . .	36·5	40*	37	99%
Zygomatic breadth . . .	62*	90*	56·5	
Mastoid breadth	58*	61	44	
Maximum nasal length. . .	47	—	28	168%
Maximum nasal breadth . .	17	—	20	85%
Minimum nasal breadth . .	14	—	16	87%

* Measurement estimated. The severe dorso-ventral crushing of No. 982.'47 has somewhat exaggerated the expansion, particularly of the zygomatic arch. Proportion $= \frac{Megapedetes \times 100.}{Pedetes.}$

Lateral aspect. (Plate I, fig. 1 ; Text-fig. 3).—The upper incisors are relatively larger than those of *Pedetes*, forming arcs of a circle of 56 mm. diameter, whereas in the Recent genus the arcs are of a 36 mm. circle. The vertical height of the skull, however, is relatively less, consequently the ridge formed by the incisor socket extends almost to the dorsal surface, whereas in *Pedetes* the top of the curve reaches only two-thirds of the muzzle height. The nasal bones lack the anterior lateral wings of *Pedetes*, and the lateral walls of the nasal aperture are thus formed by the curved ridges of the pre-maxillae enclosing the incisor sockets. The incisive angle is about 67°, compared with 62° in *Pedetes*. The anterior origin of the zygomatic plate is

correspondingly further back, 7 – 8 mm. behind the incisor socket, whereas in the Recent genus it arises almost over the posterior part of the socket. The plate itself is very much more massive than that of *Pedetes*. In the latter, the whole of the superior edge of the pre-maxilla is raised as a sharp ridge for the origin of the masseter medialis, which passes through the infra-orbital foramen. The ridge begins over the incisor socket just below the level of the base of the nasal aperture and is continuous with the pre-orbital process of the maxilla, and thence with the zygomatic plate. In the fossil a slight ridge is present from the anterior junction of the pre-maxilla with the nasal, and thence it extends back along the edge of the nasal to unite with the maxilla. This suggests that the masseter medialis was less highly developed in the fossil. The posterior margin of the infra-orbital foramen is slightly concave, owing to the more gradual curve of the masseter ridge above, and of the zygomatic plate below. The vertical pre-orbital bar is formed, as in *Pedetes*, by a process of the maxilla, in front, and by the malar and the lachrymal behind, but it is more slender than that of the Recent animal. In *Pedetes* the lower edge of the zygomatic plate is produced backwards almost horizontally to merge with that of the malar at the level of the alveolar edge of M^1. In the fossil the lower edge of the plate is produced downwards and backwards, and at the level of M^1 it lies below the occlusal level of the upper cheek-teeth. It appears from No. 982.'47, that there was also a downward extension of the malar below the posterior rim of the orbit, but this feature is not

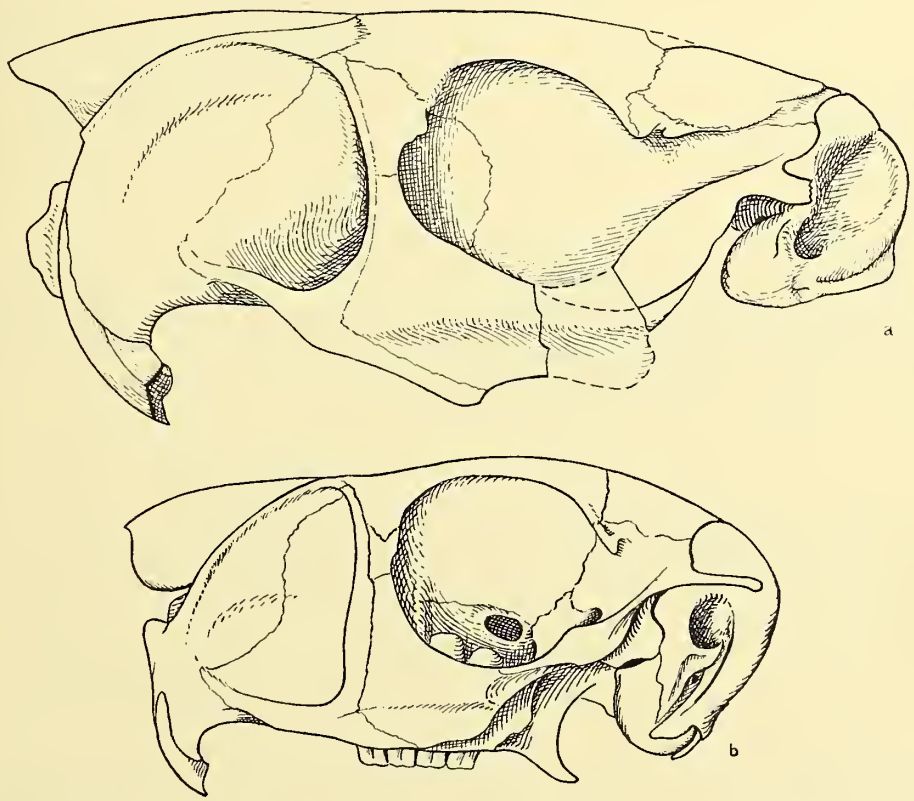

FIG. 3. (*a*) *Megapedetes*; holotype skull. × 1. (*b*) *Pedetes*. ×$\frac{1}{2}$.

preserved in the holotype. A conspicuous horizontal ridge continues the line of the zygomatic plate across the outer surface of the arch to the back of the malar-squamosal suture. Above the latter the hind part of the arch, formed by the squamosal is a broad vertical plate relatively much more massive than that of the Recent genus.

In *Pedetes* the orbit is almost circular, but in the fossil it is somewhat compressed and less regular in outline, with the lower border at approximately the same horizontal level as the lower margin of the infra-orbital depression. The lachrymal occupies the same relative position, but is enlarged posteriorly to form a distinct pre-orbital process. The post-orbital process of the squamosal is also more pronounced. In *Pedetes* the wall of the squamosal between the post-orbital and zygomatic processes rises in a smooth curve upwards and backwards to the parietal. In the fossil a prominent ridge passes back diagonally across the hind part of the parietal from the post-orbital process. The root of the zygomatic process of the squamosal is correspondingly more developed, and these two parallel ridges enclose a conspicuous trough for the temporalis muscle. As in the Recent genus, a slender posterior process from the squamosal overlies the upper part of the mastoid. The bulla is much less developed, and the tip of the lateral process of the mastoid forms the postero-inferior border of the auditory meatus, whereas in *Pedetes* this overlaps the bulla considerably below the meatus.

Measurements of the details of the lateral aspect, in millimetres, are :—

	Megapedetes	*Pedetes*	Proportion
Height of muzzle[1]	39	31	126%
Length of infra-orbital area[2]	37	25	148%
Height of infra-orbital area	31	29	107%
Length of orbit[3]	32	28	114%
Height of orbit	28	26	108%
Vertical height at first molar[4]	48	38	126%

[1] Vertical height at anterior palatal foramen.
[2] The area bounded by the masseter crest of the pre-maxilla; the anterior edge of the pre-orbital process of the maxilla, and the zygomatic plate.
[3] From the anterior rim at the lachrymal-malar junction, to the post-orbital process of the squamosal.
[4] From the occlusal surface of M^1, to the dorsal surface.

Ventral surface.—Only the anterior part of the ventral surface is preserved, apart from a detached fragment of the basi-occipital of No. 982.'47. The pre-maxillary region is more elongated than that of *Pedetes*, and the anterior palatal foramina are set slightly further back. The pre-maxillary–maxillary suture does not extend behind the level of the posterior end of the foramina, whereas in the Recent genus the suture reaches almost to the level of the inner rim of the zygomatic arch, before bending sharply forward to the foramen. From the lateral edges of the foramina the surfaces of the pre-maxillae fall away gradually to the lateral wall of the muzzle, whereas in *Pedetes* the foramina are deep-set in a median groove which extends back almost to the anterior cheek-teeth. In the fossil this groove is entirely absent, and the ventral surfaces of the maxillae are flat, and continuous with the palate. The

suture between the maxillae is raised as a distinct median ridge. In *Pedetes* the palate is arched antero-posteriorly between the cheek-teeth, and the maxillae diverge in line with the middle of M^2, whereas in *Megapedetes* there is no palatal convexity, although the divergence of the maxillae appears to have been at about the same level. Unfortunately, however, the palate is fractured immediately behind M^2 on either side, and the posterior parts with the third molars were not recovered. The posterior palatal foramina are large, and lie between the anterior lobes of the first molars. The maxillary-palatine suture is not clearly defined, but it seems to have been similar in position to that of *Pedetes*. The greatest zygomatic breadth is at the level of M^2 in the Recent genus, and the arches converge anteriorly in a gradual curve towards the upper incisors. The tooth-rows are almost parallel to the arches, and thus distinctly convergent towards the front. In *Megapedetes* the maximum zygomatic breadth appears to have been just behind the level of M^3, and anteriorly both the arches and the tooth-rows are more nearly parallel. Consequently the zygomatic plates form a more pronounced angle with the muzzle, accentuating the anterior projection of the pre-maxillary region. The basi-occipital was evidently somewhat similar to that of *Pedetes*, but the median antero-posterior crest is much more pronounced, as are the posterior lateral wings.

The palatal measurements, in millimetres, are :—

	Megapedetes	*Pedetes*	Proportion
Breadth of muzzle	17	14	121%
Pre-dental breadth of palate	13	11·5	113%
Internal palatal breadth at Pm^4	11	6·3	175%
Internal palatal breadth at M^2	12	10	120%
Length of diastema (I^1 — Pm^4)	29	19	153%
Occlusal length (Pm^4 — M^2)	14·25	12	119%

Anterior aspect.—The most conspicuous feature of the anterior aspect is the lateral compression of the pre-maxillary region, and the almost vertical muzzle walls. In *Pedetes* the nasal bones are considerably expanded, consequently the pre-maxillae are widely separated near the dorsal surface, but converge sharply to the alveolar crests of the incisors. The depression of the tips of the nasals is very slight in the fossil, and the nasal aperture is more open ; it measures 21 × 15 mm., compared with 14 × 12 mm. in the Recent genus.

Posterior aspect.—The hind end of the skull in both the holotype and in No. 982.'47 is so badly damaged that no details can be seen. It appears that the supra-occipital was less high, and the surface was flat, with no median vertical ridge. The paroccipital process is more massive, and set well behind the level of the exoccipital condyles. The foramen magnum measures approximately 17 mm. in breadth by 16 mm. in height, compared with 13·5 × 13 mm. in the Recent animal.

Mandible. (Text-fig. 4).—In addition to the holotype and No. 982.'47, two other pairs of mandibular rami are represented, but the more slender regions of the coronoid and the angle are missing in every example. On the labial surface, the masseteric

crest is much more pronounced than that of *Pedetes*. It arises anteriorly from a prominent tubercle just in front of Pm_4, and forms a conspicuous ridge lying parallel to the front of the symphysis. At the level of M_{2-3} the crest passes below the line of the incisor, at which point it is displaced outwards by some 8 mm., and thence curves inwards behind the incisor sheath to merge with the angular process. The tubercle from which the crest arises is probably produced by the combined stresses of the masseter lateralis and the temporalis muscles. A similar tubercle is present in *Pedetes*, but is less prominent. A second, smaller crest originating from the masseteric tubercle passes back almost horizontally to merge with the ascending flange of the coronoid. The whole of the outer surface of the mandible between the two crests is smooth and flat in *Megapedetes*, whereas in the Recent animal the apical regions of the persistent cheek-teeth, as well as that of the incisor, form conspicuous external tubercles. The condyle is somewhat elongated antero-posteriorly, and is not clearly differentiated from the neck of the ascending ramus on the external surface.

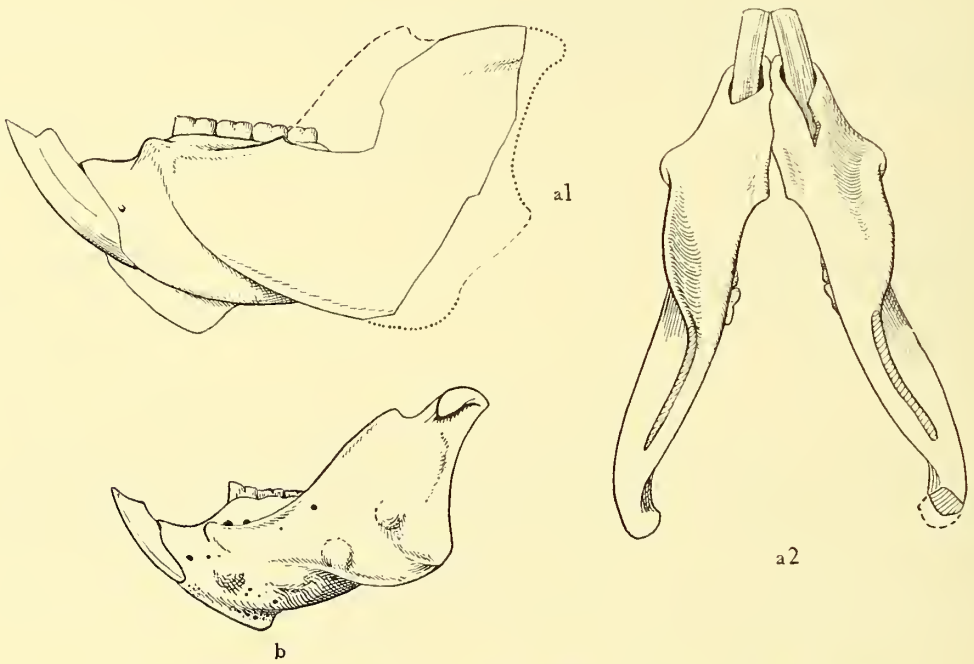

FIG. 4. (*a*) *Megapedetes*, mandible: (1) left lateral: (2) ventral. (*b*) *Pedetes*. ×1.
In (*a*)1 continuous line = left ramus of holotype; dotted line = missing parts restored from other specimens; broken line = conjectural.

The antero-external part of the condylar facet articulated with the inner part of the zygomatic process of the squamosal, and also with the posterior part of the malar. In *Pedetes* the condyle articulates only with the squamosal, and the articular area is well defined by a sharp crest overhanging the ascending ramus. The two apertures of the mental foramen are situated in much the same positions as in *Pedetes*, except that the anterior foramen is above the level of the incisor socket, whereas in the Recent animal it is over the middle of the socket. The lower part of the symphysis

is extended downwards as a prominent process in the middle line. On the lingual side the symphyseal area extends back to a point below the junction of $M_1 - M_2$. The inner surface of the body is concave below the cheek-teeth, and the bone is pitted by numerous minute foramina, though it is less reticulate than that of *Pedetes*. The inferior dental foramen is situated, as in *Pedetes*, immediately above the apical extremity of the lower incisor, but the upward extension of the condylar process is less marked. The posterior wall of the incisor socket is composed of normal cortical bone, and is not an open network as in *Pedetes*.

Measurements of the horizontal ramus, in millimetres, are :—

	Megapedetes	*Pedetes*	Proportion
Depth of ramus at Pm_4	26	16·5	158%
Depth of ramus at M_3	20	11·5	174%
Maximum length of symphysis	30	22	136%

Upper dentition. (Plate I, fig. 2 ; Text-figs. 5–6).—The upper incisors are much more powerful than those of *Pedetes*, and there is a marked lateral compression. The antero-posterior diameter is 7·5 mm. in the holotype, and the transverse diameter 4·5 mm., whereas in Pedetes the tooth measures 4 × 4 mm. A similar compression in the incisors of *Parapedetes* was described by Stromer (1926), but the dimensions (3 × 1·5 mm.) are less than half those of *Megapedetes*.

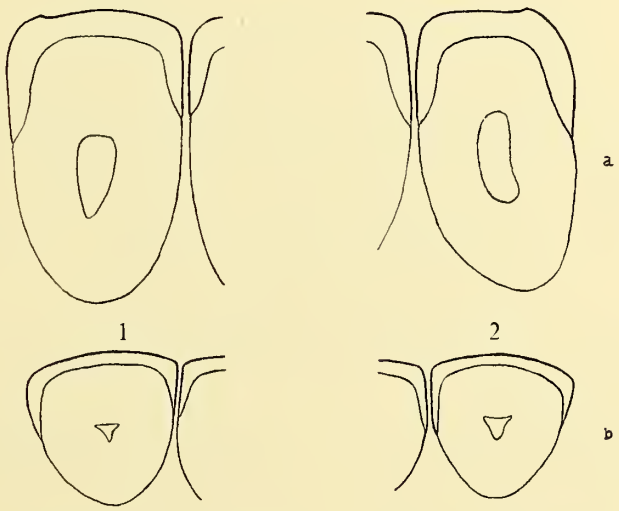

Fig. 5. Transverse sections of upper (1) and lower (2) incisors of *Megapedetes* (*a*) and *Pedetes* (*b*). × 5.

Several isolated fragments of incisor teeth were found at other sites both at Songhor and on Rusinga Island. Where possible these were sorted by curvature, and it appears that the range of size variation in the upper incisors is from 9·25 × 5 mm. to 7 × 4·5 mm. ; the average being about 8 × 5 mm. The enamel covers the anterior surface and extends over slightly less than half of each lateral wall. The mean thick-

ness of the enamel is about 0·7 mm., but it is thickened at both the anterior angles as a distinct ridge. This is particularly pronounced at the antero-external corner, whereas Stromer said that in *Parapedetes* the medial margin forms a sharp edge. Transverse sections in the apical half of the tooth show that the structure does not become appreciably modified except by the closure of the pulp cavity, and this is dependent upon the age of the individual. No trace of cementum was found in any of the specimens examined.

The cheek-teeth are simple low-crowned teeth, and not of persistent growth. The enamel is again about 0·7 mm. in thickness, and the pattern is somewhat similar to that of *Pedetes*, comprising two sub-equal lobes. In the Recent genus, however, the pattern is produced by a deep invagination of the external enamel wall of the upper teeth from crown to apex, and the age of the individual does not give rise to any appreciable modification. In *Megapedetes* the lobes are separated by a vertical invagination of the occlusal enamel, and although this is slightly deeper on the buccal surface, it does not persist to the base of the crown. Thus in the younger stages of attrition the lobes are entirely distinct; in a more worn condition they become united on the lingual side, and in very aged examples the central fold would disappear, leaving only a continuous, simple enamel ring. The latter condition is not shown in any of the upper teeth recovered, but sections cut through an isolated tooth (Text-fig. 8) indicate that this would have been the case. Both the earlier stages of attrition are well represented.

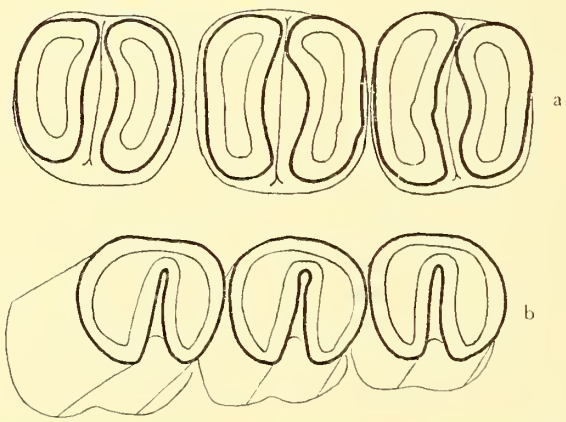

Fig. 6. Right upper anterior cheek-teeth of *Megapedetes* (*a*) and *Pedetes* (*b*). × 5.

The anterior tooth is fully molarised, and the patterns of both upper and lower cheek-teeth are so similar that isolated crowns cannot readily be distinguished unless some recognisable part of maxilla or mandible is still attached. Consequently it is impossible to determine whether or not the upper third molar is represented in the collection. In *Pedetes* the transverse enamel folds of the cheek-teeth are filled with cementum, but in *Megapedetes* no cementum has been found in any of the teeth. The roots of the upper teeth are united for about half their total length, and thereafter that of the antero-external corner becomes isolated, sometimes fusing again with the

remainder at the extreme tip. The measurements of the three anterior upper cheek-teeth of the holotype, in millimetres, are as follows :—

		Megapedetes		*Pedetes*
		Left	Right	
Pm^4	Length	4·5	4·5	3·75
	Breadth	4·7	4·7	3·8
M^1	Length	4·5	4·5	3·7
	Breadth	5·25	5·1	3·7
M^2	Length	4·5	4·6	3·7
	Breadth	5·25	5·1	3·6

In addition to the holotype, two maxillary fragments were recovered from Rusinga Island, with $Pm^4 - M^1$, and $Pm^4 - M^2$ respectively. These are slightly larger than those of the holotype, although similar in general pattern. Their dimensions, in millimetres, are :—

		R.1.	R.110.
Pm^4	Length	6·0	5·4
	Breadth	5·4	5·4
M^1	Length	5·8	5·6
	Breadth	6·25	6·2
M^2	Length	5·0	
	Breadth	6·25	

Lower dentition. (Plate I, fig. 3 ; Text-figs. 5 & 7).—The lower incisor forms an arc of a circle of about 75 mm. diameter. It is slightly more slender than the upper incisor, but the transverse section is almost similar in other respects. The dimensions range from 7 × 3·8 mm. to 8 × 5 mm. In *Pedetes* the incisor is an arc of a 45 mm. circle, and the transverse diameter is greater than the antero-posterior (3·6 × 3·9 mm.).

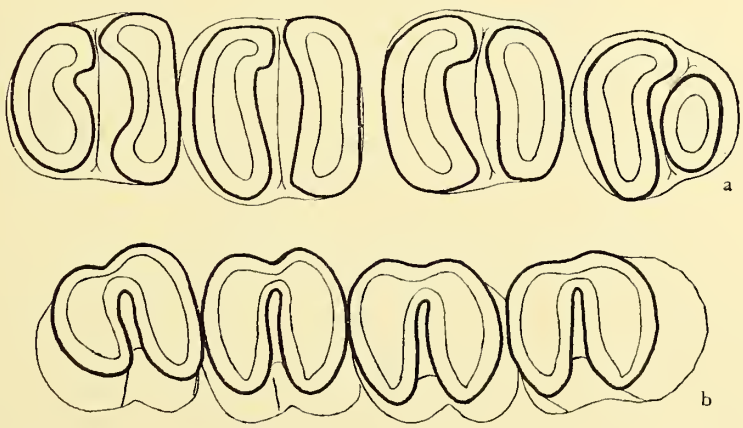

FIG. 7. Right lower cheek-teeth of *Megapedetes* (*a*) and *Pedetes* (*b*). × 5.

The lower cheek-teeth are almost indistinguishable from the upper teeth, and there is no trace of any external cementum. Stromer drew attention to the unusual condition found in *Parapedetes*, in which the deep transverse fold of the lower teeth penetrates from the buccal surface, as in the upper teeth, whereas in most rodents the orientation is reversed in the lower jaw. In *Megapedetes* the cheek-teeth are of limited growth, and the transverse fold does not penetrate the full depth of the crown, but whereas in the upper teeth it is somewhat deeper on the buccal side, in the lower teeth it is slightly deeper on the lingual side. Thus if the condition found in *Megapedetes* represents a primitive form from which persistent teeth have been derived, it seems probable that this arrangement would have given rise to the " opposed folds " of *Pedetes* rather than to the unilateral folds of *Parapedetes*.

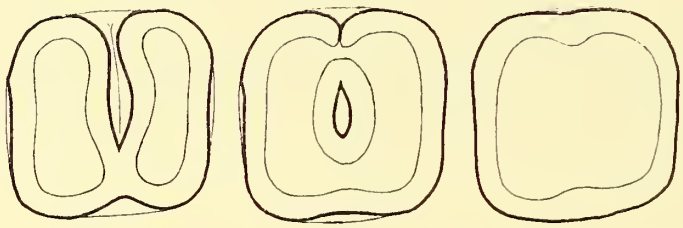

FIG. 8. *Megapedetes* (4. '51 : ? M_2 ?) molar. (1) Occlusal surface. (2-3) Sections illustrating progressive stages of wear. × 5.

In addition to the holotype and No. 982.'47, two other mandibles are included in the collection. The dimensions of all these teeth, in millimetres, compared with those of *Pedetes*, follow :—

	Holotype		982,'47		Sgr. 70'48		366.'48		*Pedetes*	
	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right
Pm_4 Length	5·0	5·0	5·8	5·7	—	—	4·8	5·0	4·25	4·2
Pm_4 Breadth	4·75	4·75	5·5	5·5	—	—	4·6	4·6	3·8	4·0
M_1 Length	4·6	4·6	5·6	5·75	5·0	4·75	4·8	5·0	3·8	3·8
M_1 Breadth	5·25	5·25	5·75	5·8	5·5	5·4	—	5·2	4·0	4·0
M_2 Length	5·0	5·0	—	—	5·0	4·8	4·8	4·8	3·9	3·9
M_2 Breadth	5·0	5·0	—	—	5·6	5·5	—	5·25	4·0	4·1
M_3 Length	4·5	4·5	—	—	—	4·2	4·4	4·5	4·0	4·0
M_3 Breadth	4·5	4·5	—	—	—	4·6	4·25	4·25	3·7	3·75
Occlusal length of series	19·5	19·5	—	—	—	—	19·75	19·5	16·5	16·5

Vertebral Column and Sacrum

Vertebrae.—The atlas vertebra (Text-fig. 9, *a*1–2) is incomplete in the holotype, but more than half of the bone is preserved in No. 982.'47. The sub-occipital foramen penetrates the lamina of the neural arch immediately above the articular surface for the condyle, and a lateral branch passes out to the anterior face of the transverse process. A subsidiary branch unites with the vertebrarterial canal, which penetrates the transverse process and emerges above the posterior zygapophysis.

The transverse processes are more developed than those of *Pedetes*, and the laminae of the neural arch are wider and almost horizontal, whereas in the Recent animal they meet at an angle of about 120°. The spinous process is a small conical projection on the anterior part of the superior arch. The inferior arch is quadrate in section, with a well marked depression for the odontoid process of the axis vertebra.

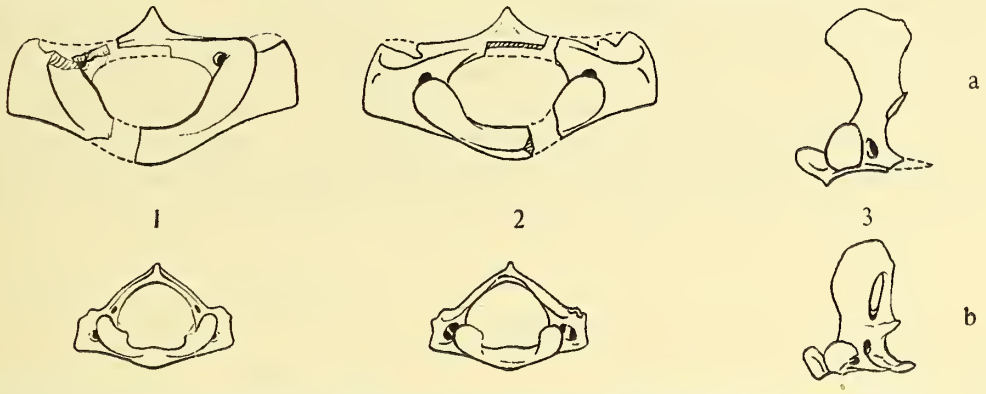

FIG. 9. Anterior (1) and posterior (2) aspects of the atlas of *Megapedetes* (*a*) and *Pedetes* (*b*). (3) Left lateral aspect of the axis of the same genera. All × 1. In *b*3 the ankylosed third cervical is also shown.

The second and third cervical vertebrae are distinct, and not ankylosed as in *Pedetes surdaster*. In the axis vertebra (Text-fig. 9, *a*3) the odontoid process is more pronounced, and the spinous process is much more massive. The posterior part of the spine is bifid, and probably came into contact with that of the third cervical. The remaining cervical vertebrae are represented by little more than the centra only. The transverse processes are much more massive, but less attenuated than those of *Pedetes*, and the neural arches are flatter.

Most of the thoracic vertebrae of the holotype are preserved, with the exception of the first, third, ninth and tenth. The number originally present is assumed to have been twelve thoracic and seven lumbar, as in *Pedetes*. The neural spines and transverse processes are somewhat stouter and less attenuated than those of *Pedetes*, but in other respects the structure is generally similar. In the Recent genus the anapophysis is rudimentary in the 9th and 10th thoracic vertebrae, while the metapophysis first appears in the 10th, and becomes united with the anterior zygapophysis in the 12th. In *Megapedetes* the development appears to have been very similar, but the metapophysis was still only rudimentary in the 11th. The centra of the last two thoracic vertebrae are sharply keeled on the ventral surface, in contrast with the flatter centra in the corresponding bones of *Pedetes*.

Parts of seven lumbar vertebrae are preserved, of which the first five are nearly complete, but lack the neural spines. The anapophysis reaches its maximum development in the 2nd and 3rd lumbars, and thereafter becomes progressively reduced, as in *Pedetes*, and is almost suppressed in the 6th. The centra of the first six lumbar vertebrae are deeper than those of the Recent genus, and the upper part is less concave. Consequently the breadth of the neural aperture is considerably greater than the height, whereas in *Pedetes* the height is nearly equal to the breadth. The ventral surfaces of the centra are laterally compressed to form a sharp median keel thoughout

the latter half of the vertebral column. This first becomes evident in the 8th thoracic vertebra as well as in the 11th and 12th. It is very pronounced in the first six lumbar vertebrae, and persists in the anterior part of the first sacral. The centrum of the seventh lumbar vertebra is not preserved. In *Pedetes* there is a slight median keel in the anterior part of some of the lumbar vertebrae, but the ventral surfaces of most of the centra are more rounded.

The sacrum comprises two fused vertebrae as in *Pedetes*. The neural spines are missing, but the anterior spine was evidently simple and relatively very slender, whereas that of the second sacral vertebra was stouter. The distal expansion of the sacro-iliac area was relatively greater. The first two caudal vertebrae are very similar to those of *Pedetes*, but the transverse and neural spines are less attenuated. The measurements of the vertebrae, in millimetres, are as follows :—

	Megapedetes	*Pedetes*
Breadth × Height of:—		
Atlas*	38·0 × 21·0	21·0 × 13·5
Axis*	24·0 × 21·0	16·5 × 17·0
2nd thoracic*	29·0	23·0
Centrum of Th.2 (posterior)	11·5 × 5·0	9·0 × 3·0
Centrum of Th.12 (posterior)	15·0 × 8·5	13·0 × 5·5
Centrum of L.4 (posterior)	18·0 × 9·5	14·0 × 6·0
Sacro-iliac expansion	50 +	38·0

* Maximum breadth across transverse processes.

The Anterior Limb

Both scapulae of the holotype are badly damaged, but those of No. 982.'47 from Rusinga Island are well preserved (Text-fig. 10, *a*1). The glenoid cavity is very

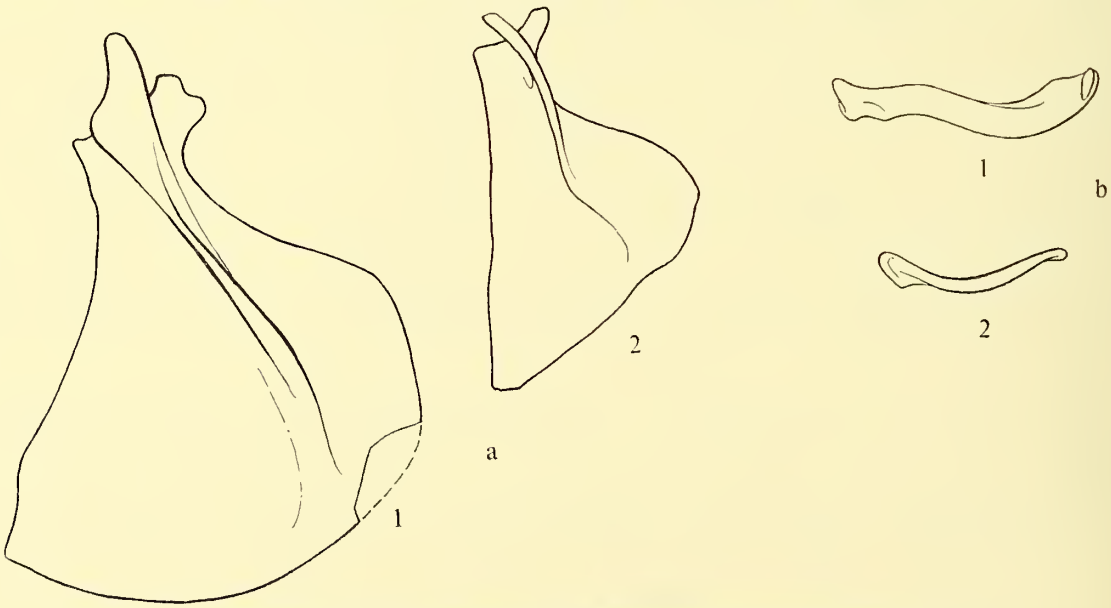

Fig. 10. Left scapula (*a*) and clavicle (*b*) of *Megapedetes* (1) and *Pedetes* (2). × 1.

similar to that of *Pedetes* except for its larger size, and the coronoid process, although broken in each case, was evidently more massive. The acromion is considerably longer and flattened, with a pronounced metacromion, whereas in the Recent animal there is no trace of the metacromion and the acromion is almost round in section. At the antero-dorsal tip of the acromion a distinct facet shows the point of articulation with the clavicle. The coracoid portion of the blade occupies a larger area than that of *Pedetes*, and the glenoid portion is more expanded posteriorly, although less elongated.

The clavicle (Text-fig. 10, *b*1) is much larger than that of *Pedetes*, and whereas the sternal end is similar, the scapular end is considerably flattened. The antero-external corner has a well defined facet for articulation with the acromion process of the scapula. The measurements of the scapula and clavicle, in millimetres, are as follows :—

	Megapedetes	*Pedetes*	Proportion
Scapula:			
a — p length of glenoid	13	8	
Tr. breadth of glenoid	9	6	
Length of glenoid edge	54	43	
Length of spine*	71	39	
Breadth of acromion at glenoid level	8	2·5	
Clavicle:			
Total length	36	22·5	160%
Depth at sternal end	6	4·25	
Depth at scapular end	7	2·5	

* From acromion tip to suprascapula border in line with spine.

The humerus (Text-fig. 11, *a*1) is well represented in all four examples from the holotype and No. 982.'47. The head is more elongated antero-posteriorly, and the great tuberosity occupies a slightly larger part of the anterior surface than in *Pedetes*. The deltoid crest is somewhat more pronounced, but the supinator ridge is less prominent and merges gradually with the shaft at a relatively higher level. In *Pedetes* the entepicondylar foramen is commonly present, but in the fossil it is present only in the right humerus of the holotype, and evidently was never developed in the left side of the same individual, nor in either humerus of No. 982.'47. There is no supra-trochlear perforation.

The radius and ulna (Text-fig. 11, *a*2 & *a*3) are well preserved in No. 982.'47, but those of the holotype are fragmentary. At the proximal end of the radius the surface for articulation with the humerus is compressed antero-posteriorly into an oval, whereas that of *Pedetes* is circular. The proximal part of the shaft is relatively stouter, and the bicipital tuberosity is very much more prominent. The distal half of the shaft is flattened as in *Pedetes* but the styloid process is scarcely developed. The surface for articulation with the scapho-lunar is relatively larger and less deeply concave. The ulna is a stouter bone, and maintains an even thickness throughout its length, whereas that of *Pedetes* is distinctly tapered towards the distal end.

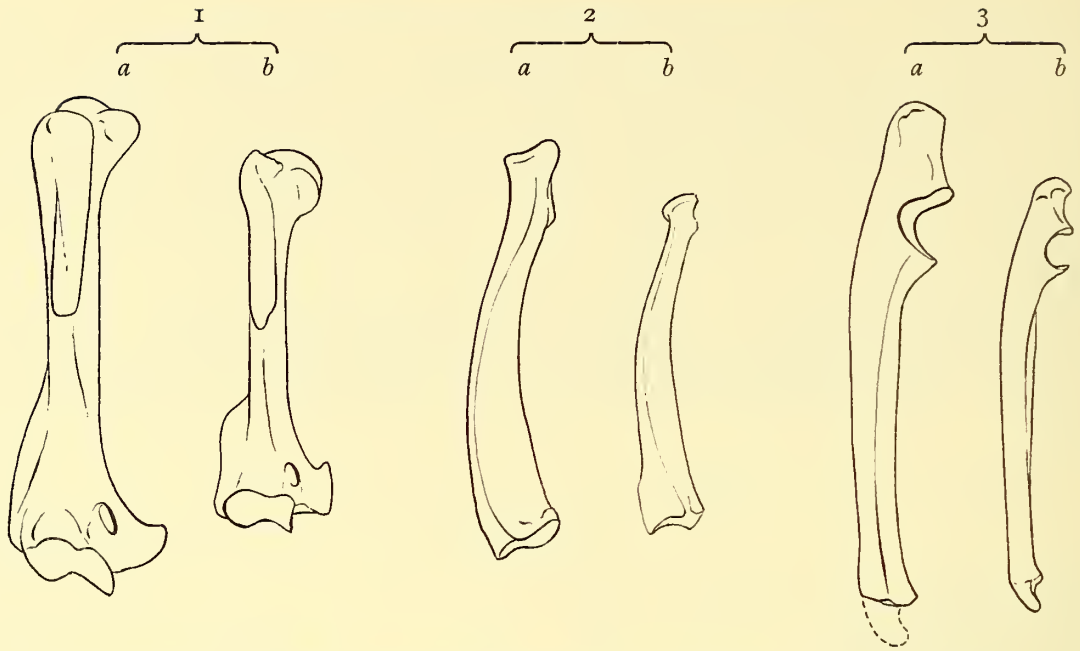

FIG. 11. Right humerus (1), left radius (2), left ulna (3) of *Megapedetes* (*a*) and *Pedetes* (*b*). × 1.

The olecranon process is more elongated, and although somewhat expanded internally, it lacks the pronounced postero-internal process of *Pedetes*. The extreme distal extremity of the bone is missing in each case.

Measurements	*Megapedetes*	*Pedetes*	Proportion
Humerus:	*mm.*	*mm.*	
Maximum length	65	50	130%
a — p length of head	14	11	
Tr. breadth of head	12	11	
Condylar breadth	21	16	
Radius:			
Maximum length	55	46	120%
Proximal end	8 × 5·5	4·5 × 4·5	
Distal end	10 × 6·5	8 × 4	
Ulna:			
Maximum length	67 +	57	117%+

Manus.—The carpus is not well represented, but most of the metacarpals and phalanges are preserved in good condition (Text-fig. 12, *a*). A striking feature in the new genus is the relatively large size of the manus. In *Pedetes* the whole of the front limb is reduced, particularly the manus, e.g., the longest metacarpal (Mc. III) is only 20% of the length of the radius. In the majority of mammals with unspecialised front limbs this proportion is from 30 to 45%, whereas in some fossorial

animals, such as *Orycteropus*, the proportion is 55%, and it may be as much as 70% in other genera in which the digging adaptation has been particularly highly developed. It is generally assumed that *Pedetes* uses its front limbs for digging, but in view of these measurements and the very weak development of the manus of the Recent genus, it seems possible that the front limb is not, in fact, of primary importance to the fossorial habits of the animal. Cuvier (1827) drew attention to this, and states that " its front feet . . . are better adapted for holding its food than for burrowing in the ground, and have every appearance of not being used for the latter purpose ".

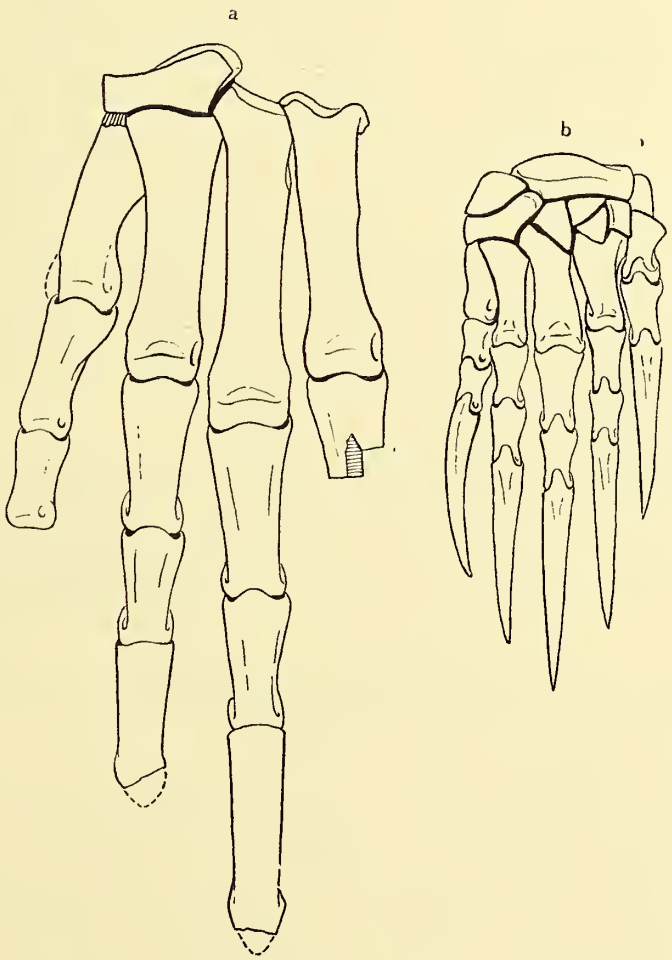

Fig. 12. Right manus; dorsal surface. (*a*) *Megapedetes*, (*b*) *Pedetes*. × 2.

In *Megapedetes* the third metacarpal is 40% of the radius, while the ungual phalanges were evidently much shorter and broader than those of *Pedetes*, and structurally the manus would certainly have been a more efficient digging implement than that

of the Recent genus. The massive clavicle and the general development of the shoulder add support to the view that the front limb was so used.

The carpus is represented only by the right unciform. This is considerably larger than that of *Pedetes*, though similar in structure. The surface for articulation with the magnum is relatively smaller, and is crescentic, whereas in the Recent genus it is circular. The area of contact with the cuneiform, on the other hand, is larger and more convex. On the lower surface the facets for the proximal ends of metacarpals IV and V merge with one another, and are not separated by a distinct ridge as in *Pedetes*.

The first metacarpal of each side is missing, but Mc. II–V of the right, and III–IV of the left side of the holotype skeleton are preserved in good condition, as well as a number of phalanges. In Mc. II the facets for articulation with Mc. I are almost exactly the same as those in the corresponding bone of *Pedetes*, and evidently the pollex was quite as fully developed. At the proximal end of Mc. II the area articulating with the overlapping portion of Mc. III is relatively larger. The greater part of the proximal end is occupied by a large concave facet for the trapezoid, and a smaller surface for the trapezium, as in *Pedetes*. The proximal surface of Mc. III is again very similar to that of *Pedetes*, but whereas in the latter the facet for the magnum consists of a smooth oblique plane, in the fossil it is concave in the middle line. The upper external corner of the bone is extended over the upper internal corner of Mc. IV, where it articulates with the unciform. Mc. IV is structurally similar to that of *Pedetes*, but the upper external corner is somewhat less expanded. The upper part of the external wall of the shaft is deeply concave, and accommodates part of the head of Mc. V. The latter is not in a good state of preservation, but appears to have no unusual features.

In *Pedetes* the main part of the distal articular surface of each of the metacarpals is semi-cylindrical, with a very prominent median keel which projects well beyond the cylindrical portion, to form the most distal point of the bone. In the fossil, a greater antero-posterior depth produces a nearly hemispherical terminal surface, and the median keel is almost confined to the posterior border. Consequently the proximal articular surfaces of the first phalanges are round, shallow cups, open at the posterior rim, whereas those of *Pedetes* are divided into two parts by a deep median groove. The distal ends of the first two phalanges are cylindrical in *Megapedetes*, while those of the Recent genus comprise two lateral ridges.

Two ungual phalanges are included ; namely those of the third and fourth digits of the right manus. The extreme tip of each is broken, but it is unlikely that the missing portion was more than a few millimetres in length. The bones are quite unlike those of *Pedetes*. The proximal articular surface is hollowed to take the semi-cylindrical distal end of the preceding bone, and the greatest breadth is transverse instead of dorso-ventral as in *Pedetes*. The plantar protuberance is stout and broad, without any lateral compression, and the upper surface evenly rounded. Immediately in front of the plantar protuberance there is a slight median constriction, and the anterior part is flattened dorso-ventrally. In the corresponding bones of *Pedetes* there is a marked lateral constriction throughout the whole length, the plantar protuberance is long and slender and the bone is sharply curved. Moreover the total length is practically equal to the combined, articulated length of the metacarpal and

first two phalanges, whereas in the fossil it was evidently less than half this length.

The comparative lengths of the metacarpals and phalanges, in millimetres, follow :—

	Mc. II	Mc. III	Mc. IV	Mc. V
Megapedetes	18	22	17·5	13·5
Pedetes	8	9	8	7·25
		Ph. 1		
Megapedetes	10	12·5	11	9·5
Pedetes	6	6·25	6·25	5
		Ph. 2		
Megapedetes	—	9	8	7
Pedetes		5·25	5	4
		Ph. 3		
Megapedetes	—	13	12	—
Pedetes		15·25	14·5	
Proportion*	Digit II	Digit III	Digit IV	Digit V
Metacarpal	225%	244%	219%	186%
Ph. 1	166%	200%	176%	190%
Ph. 2	—	171%	160%	175%
Ph. 3	—	85%	83%	—

* Proportion $= \frac{\text{Fossil bone} \times 100.}{\text{Recent bone.}}$

The Posterior Limb

A considerable portion of the left innominate is preserved (Text-fig. 13,*a*), but that of the right side is represented by the acetabulum only. The ilium is rather stouter than that of *Pedetes*, and is much more triangular in transverse section, by reason of the greater development of the origin of the rectus femoris ligament. This suggests that the extensor muscles of the hind leg were highly developed and saltatorial. The full length and expansion of the ilium is uncertain, but the proportions were evidently very much the same as those of the Recent genus. The acetabulum is also similar, but the pubic portion of the articular surface is less clearly defined. The shaft of the ischium is slender and of even thickness, whereas in *Pedetes* it is inclined to expand more widely towards the ischial spine. The obturator foramen was thus somewhat more angular. The blade of the ischium and the whole of the pubis are missing.

Both femora (Text-fig. 14, *a*1) of the holotype are well preserved, and although generally similar to those of *Pedetes*, the shaft is almost straight whereas in the

Recent animal it is sharply bowed forwards. The head is hemispherical, and the depression for the ligamentum teres is very much larger and more conspicuous. The great trochanter is large and projects 11 mm. above the level of the head. From the postero-internal border a broad flange extends downwards to unite with the

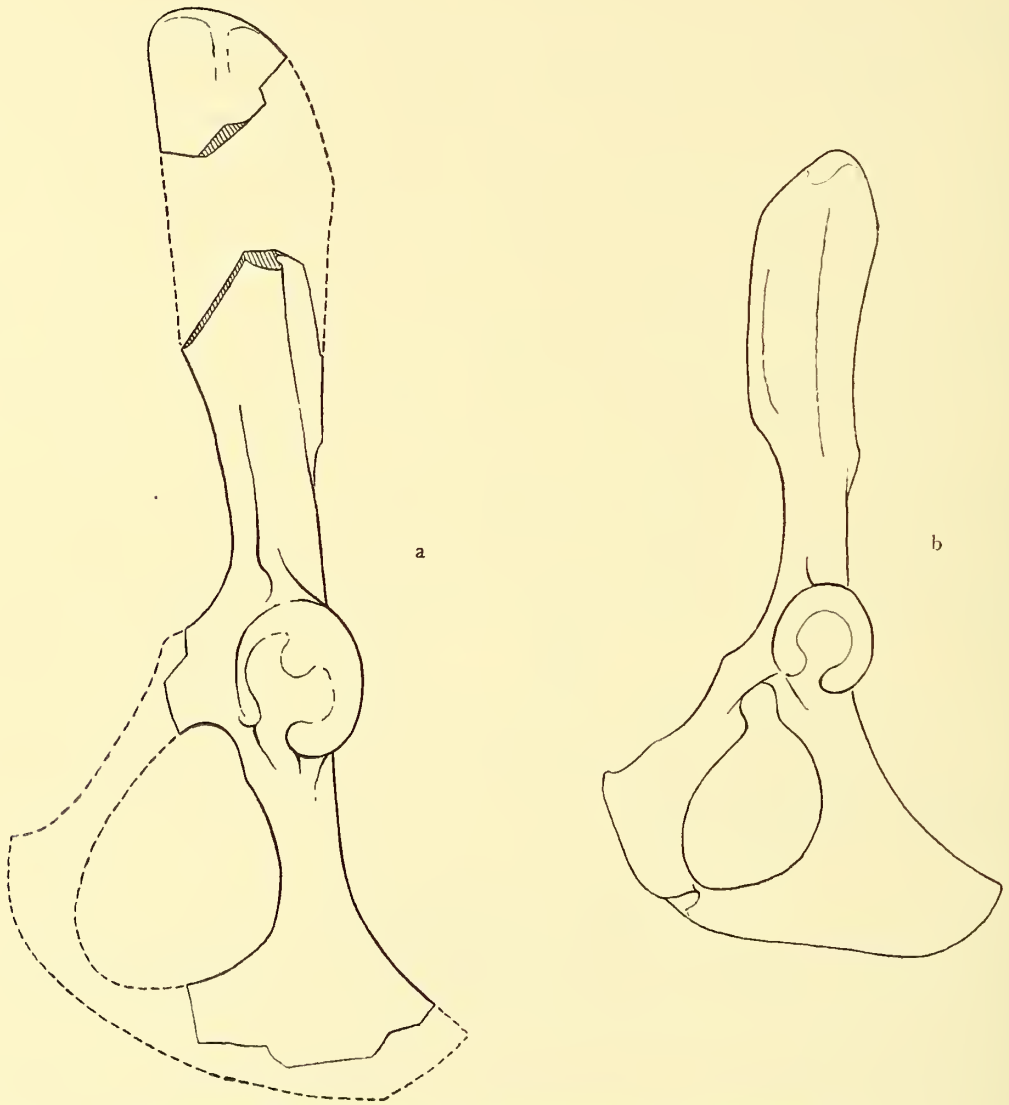

FIG. 13. Left innominate. (*a*) *Megapedetes*, (*b*) *Pedetes*. × 1.

lesser trochanter, enclosing the digital fossa in a deep recess. The general line of the trochanter continues the line of the shaft, whereas in *Pedetes* it is slightly splayed outwards, but in other respects there is close similarity. The lesser trochanter is a very prominent tubercle on the postero-internal border of the shaft about 17 mm. below the level of the middle of the head. The shaft is nearly cylindrical in its upper two-thirds, and has a slight antero-posterior flattening of the lower third. This is

less apparent in *Pedetes*. There is no trace of a third trochanter. The distal epiphysial suture is still visible, although fusion had taken place. The condyles are somewhat similar to those of *Pedetes*, but that of the outer side is rather less developed. Consequently, when placed with both condyles in contact with a horizontal surface,

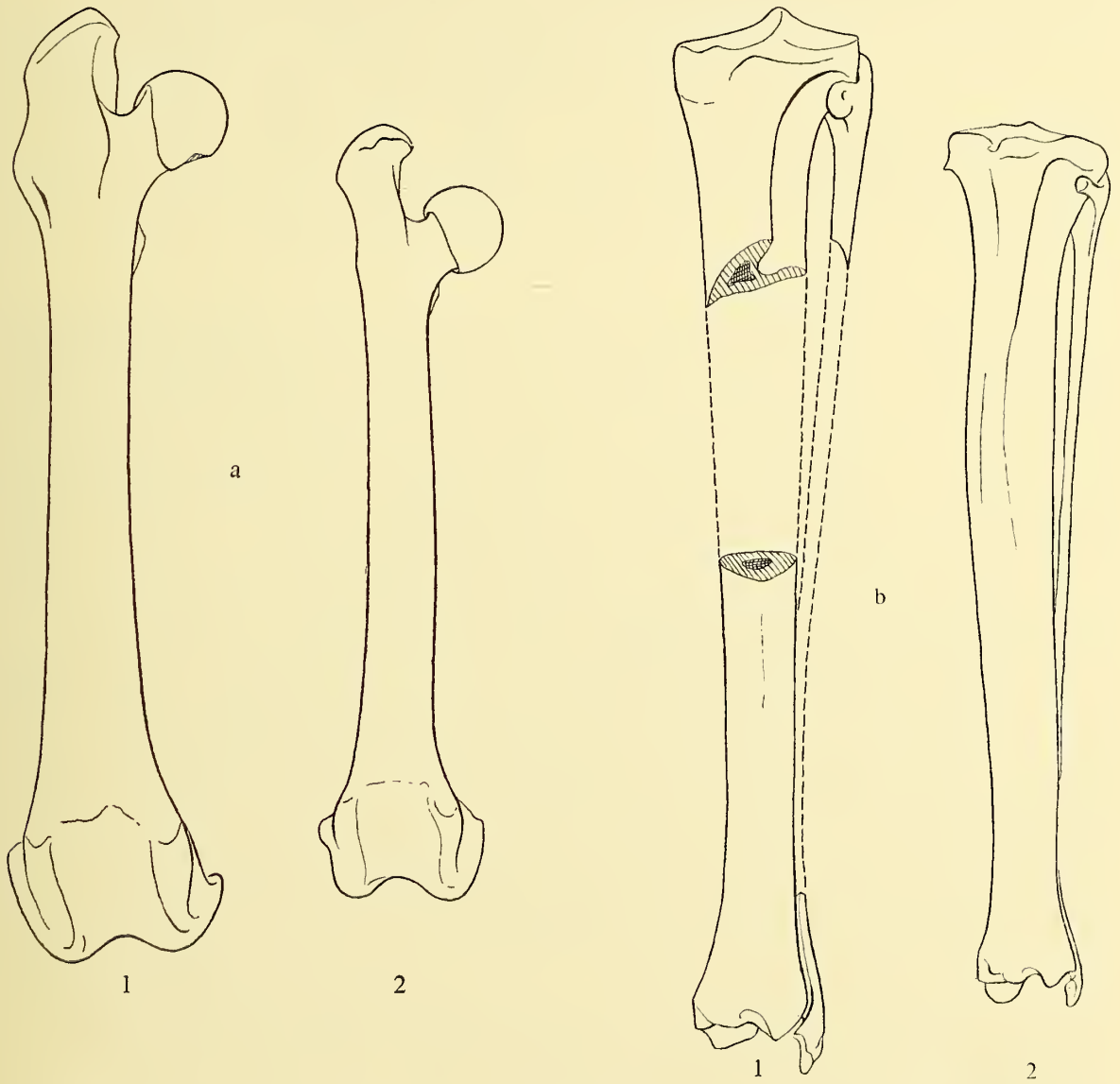

FIG. 14. Right femur (*a*) and left tibia (*b*), anterior aspects, of *Megapedetes* (1) and *Pedetes* (2). × 1.

the shaft leans at an angle of about 5° from the perpendicular, whereas that of *Pedetes* is vertical when the femur is placed in the same position. The fossil animal was thus evidently somewhat bandy-legged. Posteriorly the internal condyle is more widely expanded medially than that of the Recent genus. The facet for the patella is wide, and the marginal flanges are less prominent, but laterally the tuberosities are

slightly more inflated. The flanges of the patella facet are more oblique to the line of the shaft than are those of *Pedetes*. In the Recent animal a sesamoid bone is also developed posteriorly above the outer condyle, and the postero-superior edge is consequently flattened by contact with this bone. Evidently a similar sesamoid was present in the fossil, in which an identical facet occurs on the external condyle.

Comparative measurements of the femur, in millimetres, are :—

	Megapedetes	*Pedetes*	Proportion
Maximum length	134	108	124%
Length; head to condyles	121	98	
Median antero-posterior breadth	11	9	
Median transverse breadth	12	9	
Condylar breadth	27	21	

The patella is relatively shorter and broader than that of *Pedetes* and, although the lower extremity is damaged, it appears to have been more rounded. The upper external corner is also rounded, whereas that of *Pedetes* is angular. The dimensions are 17·5 × 12 mm., compared with 16 × 9 mm.

The rock in which the holotype was embedded was breaking up by weathering action when the specimen was found. Many blocks of the matrix had become detached, and although the majority were collected and examined, a number of bone-bearing fragments must have been overlooked. Among these were the middle sections of both tibiae and fibulae, although the proximal and distal ends of each were recovered. It is thus impossible to assess the total length of either bone, or to say whether any fusion had taken place.

The upper part of the left tibia (Text-fig. 14, *b*1) is well preserved. The proximal surface is triangular, but the anterior corner does not project so far forward as that of *Pedetes*. The tubercle formed by the attachment of the patellar ligament is also much less prominent. In *Pedetes* the facets for the femoral condyles are almost entirely separated, though united anteriorly by a narrow ridge. In the fossil the junction of the facets is a broad, flat articular surface reflecting the median extension of the internal condyle. The three crests of the upper part of the shaft are very similar to those of *Pedetes*. Part of the proximal end of the fibula is cemented to this fragment by matrix in the hollow of the antero-external wall of the shaft. The distal ends of both tibiae are in good condition ; that of the left side has part of the fibula attached. The anterior crest of the tibia shaft is still distinct, although somewhat rounded, almost to the beginning of the distal expansion, whereas in *Pedetes* it is not recognisable in the lower one-third of the shaft.

In *Pedetes* the fibula is closely applied to the postero-external crest of the tibia from about the middle of the shaft. In very young individuals the two bones may be distinct, but as age advances some degree of fusion takes place. In older examples bone-resorption occurs, which may remove a section of the fibula in the ankylosed area. There is no indication in the tibiae shaft of *Megapedetes* that fusion or resorption took place. The distal articular surface of the tibia is very similar to that of *Pedetes*.

In the majority of highly saltatorial mammals the elongation of the hind limb is brought about largely by a modification of the tibia and pes, while the femur is not markedly lengthened. The hind foot of *Megapedetes* is evidently less highly modified than that of *Pedetes*, and it may be assumed that the tibia was also less elongated. In *Macropus*, for example, the femur : tibia ratio is only about 60%, while the proportion of Mt. III : tibia is about 38%. For this reason the estimated tibia length of the fossil is based on the proportion of Mt. III : tibia in *Pedetes*. This is found to be 38%, and the length of Mt. III of the fossil is 56 mm. Thus the original length of the tibia may be estimated as $\frac{56 \times 100}{38} = 147$ mm. approx. A diagrammatic reconstruction of the fragments also suggests a length of about 150 mm.

Comparative measurements of the tibia, in millimetres, are :—

	Megapedetes	*Pedetes*
Total length	150*	135
Antero-posterior breadth of head	28	23
Transverse breadth of head	27	23
Median antero-posterior breadth of shaft	12	10
Median transverse breadth of shaft	10	10
Distal antero-posterior breadth	13	10
Distal transverse breadth	17	15

* Estimated.

The proximal end of the fibula is in poor condition, and any detailed comparison with that of *Pedetes* is impossible. An external tubercle on the expanded head is distinctly larger than that of the Recent genus, but its function is not quite clear. It may represent the origin of the soleus muscle ; this would imply a relatively greater leaping power. The fibula shaft tapers sharply below the head, to an antero-posterior thickness of 4 mm. just above the lower fracture. The proximal fragment measures 25 mm. in length, and the distal fragment 24 mm. The latter is cemented to the lower end of the tibia shaft by matrix, and is approximately in its correct position. The articular facets are similar to those of *Pedetes*, but in the Recent genus the expanded portion is almost at right angles to the shaft, whereas in the fossil it is more nearly straight. The lower portion of the shaft is almost cylindrical in section, and about 2·5 mm. in diameter.

Pes.—The most striking and significant feature of the hind foot is a well developed hallux. In the Recent *Pedetes* and in the Miocene *Parapedetes* Stromer, the first digit is entirely suppressed and the internal cuneiform is reduced to a thin splint, which articulates with the astragalus and the second metatarsal, and supports the medial side of the tarsus. Practically the whole of the left hind foot of the holotype was recovered in a single block of matrix, with all the bones articulated except for some of the distal phalanges. The right hind foot from this skeleton was scattered, but several bones, including the first metatarsal, were found in the débris. In addition to the holotype, three bone-bearing pebbles, evidently derived from the deposits, were collected from the surface of the Miocene sediments on Rusinga Island in 1932.

These contained the united astragalus and calcaneum of the right side, and the complete metatarsus of both sides. In each of the latter the first metatarsal is fully developed and identical with those of the holotype. Another significant feature is that despite the larger size of *Megapedetes* the tarsus (Text-fig. 15*c*) and metatarsus are very little longer than those of *Pedetes*. Thus although the animal was already highly saltatorial, the hind foot had not yet reached a comparable degree of specialisation. The short, compact tarsals suggest a heavier animal, and the greater breadth of the articular surfaces would give the requisite increase in stability.

The astragalus (Text-fig. 15, *a*1) is somewhat similar to that of *Pedetes*, but lacks the great attenuation of the neck, while the transverse diameter of the proximal end is relatively broader. The surface for articulation with the tibia consists of the usual two curved ridges. In *Pedetes* the valley separating the ridges is slightly deeper, with the deepest point nearer to the middle of the transverse breadth. In the fossil the medial flange is more compressed and the lateral flange more rounded, with the

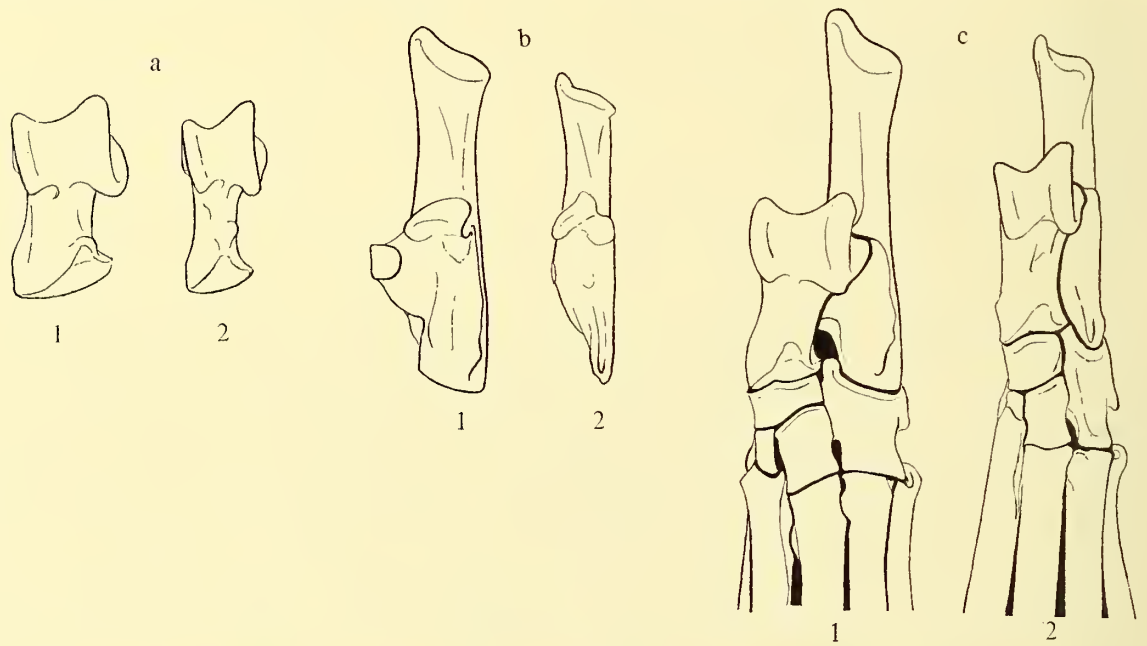

Fig. 15. Left astragalus (*a*), calcaneum (*b*), and tarsus (*c*) of *Megapedetes* (1) and *Pedetes* (2). × 1.

deepest point of the valley nearer to the medial side. On the external surface, the facet for the fibula is flat, whereas in the Recent genus it is concave owing to an overhang of the upper part of the external tibial flange. On the ventral surface below the external tibial flange there is a deep socket for the principal dorsal articular facet of the calcaneum. In *Pedetes* this socket extends diagonally across the lower surface for about three-quarters of the transverse breadth, but in the fossil it is less elongated, and occupies only about one-half of the lower surface. The second facet for the calcaneum occupies a large part of the ventral surface of the neck, and is much larger than the corresponding facet in *Pedetes*. It is separated from the principal calcaneal articulation by a deep valley which passes diagonally across the base of the neck to

to the lower extension of the tibial facet. In the Recent genus the medial extension of the principal calcaneal facet separates the diagonal valley from the tibial articulation. The neck is shorter and stouter than that of *Pedetes*. The medial wall of the bone is produced downwards below the level of the ventral surface as a conspicuous flange, on the anterior part of which is a facet for the posterior process of the internal cuneiform. The distal surface of the head is mainly occupied by the facet for the navicular, but a smaller facet truncating the antero-external corner makes contact with the cuboid. In *Pedetes* the cuboid articulation is confluent with that of the navicular, and the antero-external corner of the astragalus almost comes into contact with the calcaneum. The comparative measurements, in millimetres, are :—

	Megapedetes	*Pedetes*	Proportion
Maximum length*	27·5	25·5	108%
Length of medial side	25	23	109%
Proximal transverse breadth	15	11	136%
Length of neck and head	14·5	14·5	100%
Transverse breadth of head	10·5	9	117%

* Antero-internal : postero-external diagonal.

The calcaneum (Text-fig. 15, *b*1) is relatively shorter and broader than that of *Pedetes*, but the tuber calcis is greater in proportion. A prominent central eminence forms the principal articulation with the astragalus ,while the second astragalar facet is set much further out from the shaft on the medial side of the bone. In *Pedetes* this second facet is scarcely offset from the shaft. The distal articular surface for the cuboid is larger than that of the Recent genus owing to the greater breadth of the anterior part. Taking the central eminence as a fixed point, the anterior part is exactly the same length in the two genera, but the tuber calcis is 8 mm. longer in the fossil. The dimensions of the calcaneum, in millimetres, are :—

	Megapedetes	*Pedetes*	Proportion
Maximum length	47	39	120%
Maximum depth*	16	12	133%
Maximum breadth	16	9·5	168%
Length of tuber calcis	26	18	144%
Depth of tuber calcis	14	9·5	147%
Breadth of tuber calcis	10	7·5	133%

* Including central eminence.

The navicular is of the same general form as that of *Pedetes*, but is appreciably less elongated. The main cup is wider and shallower, and the recess for the proximal process of the cuboid is less conspicuous. On the ventral surface the plantar protuberance is more massive, but considerably shorter. In the Recent genus there is a second small facet for the cuboid on the side of the plantar protuberance, but this is not present in the fossil. The posterior process of the first cuneiform (C.1) overlies

the medial surface of the protuberance, and, although there is no point of contact on the navicular, the trough in which it lies is considerably deeper in the fossil to allow for the more massive cuneiform necessitated by the presence of a functional hallux. The facets for C.2 and C.3 are similar to those of *Pedetes*. In the Recent genus C.1 comes into contact with the extreme antero-internal corner of the navicular, where a minute articular facet is visible. Comparative measurements of the navicular, in millimetres, are :—

	Megapedetes	*Pedetes*	Proportion
Maximum antero-posterior depth	15·5	13	119%
Transverse breadth	11+	8	137%
Anterior proximo-distal thickness	5·5	6	92%
Length of plantar protuberance	12	15	80%

The first, or internal cuneiform (Text-fig. 16, a1) consists of a somewhat rectangular plate, with a long process extending back from the posterior proximal corner. An oval articular facet at the proximal tip of the process shows the point of contact with the head of the astragalus, as in *Pedetes*, but the body of the process is stouter and almost cylindrical. The anterior proximal corner is also somewhat enlarged, and has a concave facet for articulation with the second cuneiform. A corresponding facet is also present in *Pedetes*, but is flat and considerably smaller. The distal end of the bone is concave, with a well defined surface for articulation with the first metatarsal. On the medial wall there is a prominent tubercle for the insertion of the tibialis anticus ligament. There is no facet to indicate any articular contact with the second metatarsal. In *Pedetes* the suppression of the hallux has brought about a reduction of C.1 to a slender splint with a mean thickness of about 1 mm. At its distal end, however, it articulates with the shaft of Mt. II. Comparative measurements of the first cuneiform, in millimetres, are :—

	Megapedetes	*Pedetes*	Proportion
Total length (including process)	20	18·5	108%
Length of process	10·5	9	117%
Median depth	7	6	116%
Median thickness	3	1	

The second cuneiform is almost entirely enclosed by the four adjacent bones. The exposed anterior surface is nearly square, with the antero-distal corner truncated. The proximal surface is entirely occupied by a facet for articulation with the navicular, and is gently concave from front to back. The medial surface is overlaid by C.1, and has a central hollow facet for the reception of the articular prominence of the latter, whereas in *Pedetes* this articulation is small and flat. The distal surface is somewhat expanded medially owing to an extension of the proximal end of Mt. II with which it articulates. This facet is concave antero-posteriorly, and transversely convex.

A small facet on the antero-external corner marks the only articular contact with C.3. The dimensions, in millimetres, are :—

	Megapedetes	*Pedetes*	Proportion
Anterior proximo-distal length	5	4	125%
Maximum antero-posterior depth	10	7·5	133%
Transverse breadth	4·5	3	150%

The third, or external cuneiform is very similar to that of *Pedetes*, and although greater in volume, is very little longer. The anterior surface is almost rectangular and the transverse section is triangular. The upper surface has a rounded convex facet for articulation with the navicular. This is relatively much larger than that of *Pedetes*. The distal end is entirely occupied by the surface for articulation with Mt. III. The internal surface has three small articular facets, of which the antero- and postero-distal come into contact with the upper part of the shaft of Mt. II. The third internal facet articulates with C.2. The upper part of the external surface has a large L-shaped facet for the cuboid, whereas in *Pedetes* the two arms of this facet are widely separated from one another. The dimensions of the third cuneiform, in millimetres, are :—

	Megapedetes	*Pedetes*	Proportion
Proximo-distal length	9	8·5	106%
Proximo-distal breadth	6·25	5	125%
Antero-posterior depth	10	8	125%

The cuboid is relatively short and broad, with a much larger articular surface for the calcaneum than that of *Pedetes*. The upper internal corner extends upwards in a long process between the head of the astragalus and the distal end of the calcaneum. In the Recent genus this process is relatively less prominent, and, as noted above, the upper articular surface is confluent with that of the navicular and directly opposed to the distal end of the astragalus. The medial surface of the process has the astragalar facet at the proximal tip, followed by three small facets for the navicular and an L-shaped area of contact with C.3. In *Pedetes* the proximal end of Mt. III projects slightly above that of Mt. IV. Consequently the lower medial surface of the cuboid shows distinct facets for articulation with the upper-external part of the shaft of Mt. III. In the fossil there is no such discrepancy between Mt. III–IV, and the cuboid does not, therefore, articulate with Mt. III. The distal end is largely occupied by the facet for Mt. IV, but the antero-external corner, which is more widely expanded than that of *Pedetes*, evidently gave some degree of support to Mt. IV. Furthermore, the fifth metatarsal of the fossil has a prominent posterior proximal process which overlaps the outer wall of the cuboid and forms a distinct articular facet at the postero-distal corner. There is no such overlap in the Recent genus, and no facet for Mt. V exists on the outer wall of the cuboid. The posterior part of the

proximal surface has a well defined secondary articular facet for the calcaneum. On the postero-internal wall of the bone there are two very prominent tubercles, probably for the attachment of the calcaneo-cuboid ligaments. The dimensions of the cuboid, in millimetres, are :—

	Megapedetes	*Pedetes*	Proportion
Proximo-distal length	16	16	100%
Transverse breadth	11	7	157%
Antero-posterior depth	10·5	9	117%

The examples of the articulated metatarsus show that the hind foot was almost mesaxonic. Mt. II is appreciably longer than Mt. IV, but since the proximal end is considerably above that of Mt. IV the distal ends reach to almost the same level. The distal end of Mt. I is about 2 mm. more proximal than that of Mt. V, and the extra phalanx would have made the fifth digit somewhat longer than the hallux. This arrangement might well have given rise to the condition found in *Pedetes* simply by suppression of the first digit. In *Parapedetes* the fourth metatarsal is the longest, and the hind foot is thus more paraxonic, with the axis between the third and fourth digits.

The proximal end of each metatarsal is roughly in the form of an isosceles triangle with the short base to the front. When articulated they form segments of a circle of about 25 mm. diameter. Thus when viewed from the front the upper ends of the lateral metetarsals are almost hidden behind Mts. II and IV, which are themselves facing somewhat outwards from the antero-posterior mid-line of Mt. III. As a compensation for this arrangement the shafts of the lateral metatarsals, particularly Mts. II and IV, have an axial twist to bring the distal heads more nearly into alignment.

The third and fourth metatarsals are nearly straight, but the first, second and fifth curve slightly outwards from the axis of the foot. The shafts of the three central metatarsals are nearly cylindrical in transverse section, with a faint indication of a quadrate form. Those of the two lateral metatarsals are distinctly flattened axially, and rounded laterally. The distal articular surfaces are somewhat barrel-shaped, with a prominent median keel on the posterior face, separating the two sesamoid bones of the flexor tendons. This keel is confined to the posterior part, and is not visible from the anterior aspect. The shaft is deeply hollowed at either end of the barrel-articulation.

The shaft of Mt. I (Text-fig. 16, a1) is rounded on the medial side, but somewhat flattened along the axial wall, which was closely applied to Mt. II. The proximal end is considerably expanded ventrally as a pointed process which rises above the level of the C.1 articulation. The surface in this region is roughened, indicating a close ligamentous connection with the corresponding posterior flange of Mt. II, but only a small and indistinct median articular facet is visible. A second proximal process is present arising from the medial wall of the shaft. The articular surface for C.1 lies between the posterior and the lateral processes and extends downwards to the antero-external crest of the shaft. The general line of the shaft is

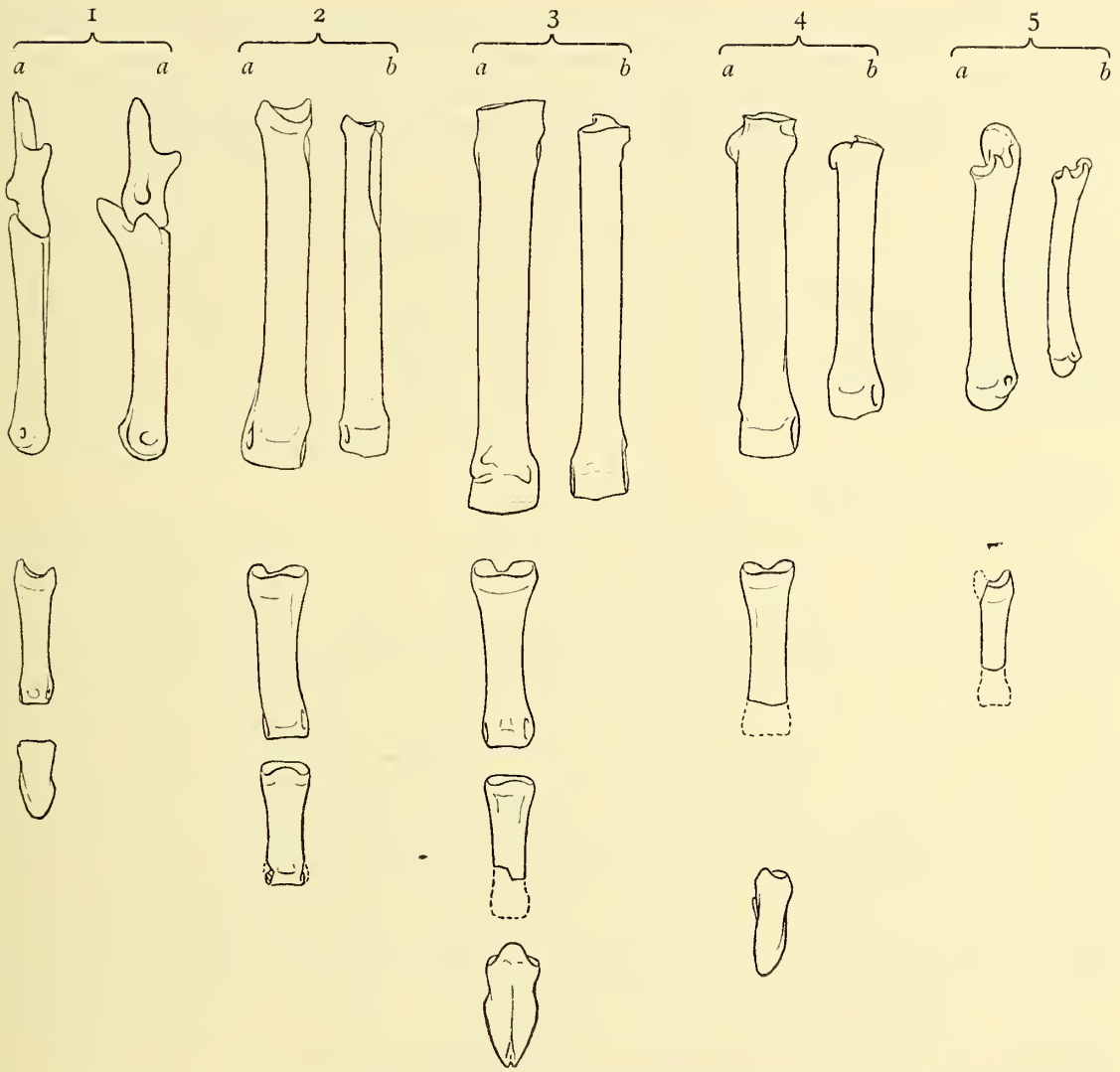

FIG. 16. Left cuneiform 1, Mt. I and phalanges, anterior and medial aspects (1); Mt. II–Mt.V and phalanges (2–5), anterior aspect, of *Megapedetes* (*a*) and *Pedetes* (*b*). × 1.

straight, but the distal articular end is somewhat splayed outwards from the axis of the foot. The measurements of the first metatarsal, are :—

Maximum length	34 mm.
Median antero-posterior thickness . .	5 mm.
Median transverse breadth . . .	4 mm.

The proximal end of Mt. II (Text-fig. 16,*a*2) is much attenuated, with a prominent posterior flange separating the proximo-posterior processes of the first and third metatarsals. The proximal articular surface is the counterpart of the distal end of C.2; convex antero-posteriorly, and transversely concave. The medial wall is considerably roughened for some 9 mm., by the ligamentous attachments of Mt. I. There is, of course, no trace of the facet found in the corresponding bone of *Pedetes* for articulation with the distal end of C.1. On the external side articular facets show the contact

with C.3. Below this the shaft is somewhat hollowed, and conspicuously roughened, but there are no smooth areas of articulation. Thus the connection between Mts. II–III was evidently ligamentous. It is possible that a bony articulation may have existed between the posterior processes, but this part of each bone is damaged in the holotype. Comparative measurements of Mt. II, in millimetres, are:—

	Megapedetes	*Pedctes*	Proportion
Maximum length	50	45	111%
Proximal antero-posterior depth	13	8	162%
Proximal transverse breadth	6·5	4·5	144%
Median antero-posterior depth	5·5	5	110%
Median transverse breadth	5·5	4·5	122%
Distal antero-posterior depth*	8	6·5	123%
Distal transverse breadth	8	6·25	128%

* Including posterior median keel.

The upper articular end of Mt. III (Text-fig. 16, *a*3) is very similar to that of *Pedetes*, though more deeply indented on the outer margin. This is due to the very deep depression in the upper external region of the shaft. The median rim of the articular surface is also slightly hollowed, but immediately below the edge the wall of the shaft is considerably inflated and roughened by the ligament attachments from Mt. II. From the anterior aspect the plane of the upper facet for C.3 is oblique to the shaft, as in *Pedetes*, with the upper external corner about 1·5 mm. higher than the upper medial corner. On the posterior surface the tubercle of origin of the adductor pollicis is much more massive than that of *Pedetes*. Below the antero-external corner a large concave facet on the upper wall of the shaft articulates with the medial articular process of Mt. IV. An additional facet for Mt. IV occupies the external wall of the posterior process and tubercle, as in the Recent genus. In the left foot of the holotype the two distal sesamoid bones of the flexor tendons are still *in situ*. These are kidney-shaped, with sharp posterior crests. The axial surfaces are flat, and meet in a wide V-shaped valley over the posterior median keel of the metatarsal. Comparative measurements of Mt. III, in millimetres, are :—

	Megapedetes	*Pedetes*	Proportion
Maximum length	56	51	110%
Proximal antero-posterior depth	12·5	9·75	128%
Proximal transverse breadth	8·5	6·5	131%
Median antero-posterior depth	5·75	5	115%
Median transverse breadth	6·5	5	130%
Distal antero-posterior depth	7*	6	116%
Distal transverse breadth	8	7·25	110%

* Estimated.

The upper articular facet of Mt. IV (Text-fig. 16, *a*4) occupies a relatively larger area than that of *Pedetes*, and overlaps the medial articular process to a greater extent. In the Recent genus the upper, cuboid facet is almost confluent with that of the medial process which comes into contact with Mt. III. In the fossil the proximal and

medial facets are much more distinct, and in articulation the proximal surfaces of Mts. III–IV are at the same level. On the external wall, the upper part of the shaft is again deeply excavated to take the principal upper articulation of Mt. V. The posterior process of Mt. IV projects considerably beyond the backward limit of Mt. V, and the posterior tip of the process is wedge-shaped, with a sharp vertical crest separating two distinct articular surfaces. That of the medial side is evidently the point of contact with the posterior process of Mt. III. The external facet, however, cannot represent articular contact with either the cuboid or with Mt. V, and it probably made contact with a sesamoid bone in the tendon of peroneus longus muscle. In the holotype the two distal sesamoids are again *in situ*, together with most of the first phalanx. The external sesamoid is distinctly the smaller of the two, but in shape they are similar to those attached to Mt. III. Comparative measurements of the fourth metatarsal, in millimetres, are :—

	Megapedetes	*Pedetes*	Proportion
Maximum length	46	38·5	119%
Proximal antero-posterior depth	10	7·5	133%
Proximal transverse breadth	8·5	7	121%
Median antero-posterior depth	4·5	4·5	100%
Median transverse breadth	5	4	125%
Distal antero-posterior depth	7·75	6	129%
Distal transverse breadth	6	6	100%

The fifth metatarsal (Text-fig. 16, *a*5) is relatively more massive than that of *Pedetes*. The upper medial wall of the shaft has a prominent rounded tubercle which fits into the articular pit on the outer wall of Mt. IV. On the lateral side of this tubercle and at a slightly higher level, the proximal facet evidently came into contact with a part of the distal end of the cuboid to give additional support to the digit. The outer wall of the shaft is produced upwards considerably above the level of the main articular area, particularly in the posterior region. This process overlaps the postero-distal part of the cuboid, and the point of articulation is visible as a smooth facet on each bone. In *Pedetes* there is no outer wall bounding the proximal articular area, but only a small pointed process at the antero-external corner and a more massive posterior process. The latter rises only slightly above the level of the articular area and does not come into contact with the outer surface of the cuboid. Moreover the shaft of the metatarsal is markedly flattened transversely, whereas that of the fossil is stouter and more nearly cylindrical. Measurements of Mt. V, in millimetres, are :—

	Megapedetes	*Pedetes*	Proportion
Maximum length	37	28	132%
Proximal antero-posterior depth	7	7	100%
Proximal transverse breadth	6·5	4·5	144%
Median antero-posterior depth	4·5	3·75	120%
Median transverse breadth	3·75	2	187%
Distal antero-posterior depth	6·25	5	125%
Distal transverse breadth	6	3·75	160%

A selection of phalanges (Text-fig. 16) was recovered attached to, or associated with the left hind foot of the holotype, but the ungual phalanges are missing with the exception of one which appears to be of the first digit.

The first phalanx of each digit is very similar to that of *Pedetes*. The proximal articular surface consists of a wide, shallow cup, with a median groove in the ventral half, into which fits the posterior median keel of the metatarsal when the digit is flexed. A prominent tubercle on either side of this groove articulated proximally with the corresponding sesamoid. The shaft is slender and somewhat flattened dorso-ventrally in the second and third digits, but those of the first, fourth and fifth digits have a very slight lateral compression. The distal articular head is somewhat depressed, with the smooth part of the facet almost confined to the distal and ventral surfaces. The distal articulation is semi-cylindrical with a faint trace of a median depression, but this is not reflected in the hollow proximal ends of the second row of phalanges. The ungual phalanx is severely abraded and the details of its structure are obscured. It was evidently flattened dorso-ventrally and expanded in much the same way as those of *Pedetes*, and there is an indication of a longitudinal bony ridge reinforcing the ventral surface. Comparative measurements of the phalanges, in millimetres, are :—

	First phalanx			
	Digit I	Digit II	Digit III	Digit IV
Maximum length	18·25	24 (18·25)	25 (20)	22 (17·5)
Proximal antero-posterior	5·75	7 (5·5)	7·25 (6)	6·25 (5·5)
Proximal transverse	5·5	8 (7)	9 (7·25)	7 (6)
Median antero-posterior	4	5 (4·5)	5 (4·25)	5 (4)
Median transverse	3·75	5·5 (3·75)	5·5 (4·75)	4 (3·5)
Distal antero-posterior	3·75	4·25 (4·25)	5 (4·25)	4 (4)
Distal transverse	4	6 (4·5)	7 (6)	5·25 (4·75)
	Second phalanx			
Maximum length		16 (11·5)		14 (11·5)
Proximal antero-posterior		6 (5·5)		6 (5·5)
Proximal transverse		6·5 (5)		6 (5·25)
Median antero-posterior		4·5 (3·5)		4 (3·75)
Median transverse		5 (3·75)		4·25 (3·5)
Distal antero-posterior		4 (4)		3·5 (4)
Distal transverse		5·25 (4·25)		5 (4·25)

The figures in brackets are the corresponding measurement in *Pedetes*.

In addition to the holotype material described above, two isolated ungual phalanges were recovered from Rusinga Island (No. 374.'47 from the R.1 series, and No. 58.'48 from R.106). These examples are included in Text-fig. 16 together with the phalanges of the holotype. The first of these is from a central toe, while the other is either that of the second right, or of the fourth left digit. In *Pedetes* the ungual phalanges of the second and fourth digits are practically mirror-images of one another,

and it is thus impossible to place this bone more exactly. For convenience of description it is taken to be that of the left fourth digit.

The central ungual phalanx is the same length as that of *Pedetes*, but it is appreciably deeper and stouter. The plantar surface is flat or very slightly concave, and the plantar protuberance is almost in the same plane as the rest of the lower surface. A conspicuous lateral fold on either side of the basal surface separates the protuberance from the distal ungual portion. In *Pedetes* the protuberance is somewhat below the level of the lower distal surface, and the lateral constriction is much less distinct from the ventral aspect, owing to the greater expansion of the distal part of the protuberance. In the fossil the lateral walls of the bone are flat and meet one another at an angle of about 60° in a sharp dorsal keel, whereas in the Recent genus the angle is wider and the keel more rounded. The prominence of the keel, however, evidently develops as the age of the animal advances. The extreme distal tip of the dorsal keel bifurcates both in the fossil and in the Recent genus, and the bone is symmetrical about the middle line.

The ungual phalanx of the fourth digit is asymetrical, with the medial wall nearly vertical and the dorsal keel consequently more towards the medial side. The plantar protuberance is large, and lies distinctly below the level of the distal part. It is separated from the body of the bone by deep lateral grooves, whereas in *Pedetes* there is no such clear demarcation. The lateral constriction is again present, but from the ventral aspect it is somewhat obscured by the protuberance. In *Pedetes* there is a slight constriction on the medial side only. Comparative measurements, in millimetres, of these phalanges are :—

	Digit III : ph. 3		Digit IV : ph. 3	
	Megapedetes	*Pedetes*	*Megapedetes*	*Pedetes*
Maximum length . . .	15·5	15·5	13·25	11·5
Maximum breadth . . .	7	6·5	5·25	5
Maximum depth	6·5	5	6	4·5

Discussion

Stromer (1926) pointed out that *Parapedetes* had evidently developed along somewhat different lines from *Pedetes* and concluded that in spite of the more primitive nature of some of its structural features it could not have been directly ancestral to the Recent genus. Dietrich (1942) did not agree with this view, and was of the opinion that *Pedetes* might well have been directly derived from *Parapedetes*. As far as the available evidence goes the two fossil genera must each be referred to the Lower Miocene, and must therefore have been virtually contemporary. Thus *Pedetes* cannot be a direct descendant of both, but whereas *Parapedetes* exhibits certain features which appear to represent a higher degree of specialisation, *Megapedetes* shows no indication of a comparable divergence, and is in every respect a less specialised form. For this reason the new genus is provisionally regarded as probably representing a stage in the direct evolutionary line which gave rise to *Pedetes*.

Although the angular process of the mandible is largely missing from each example, it was evidently not particularly displaced outwards, but lay immediately behind the posterior part of the lower incisor root-sheath. On the other hand the oblique ridge extending across the lateral wall of the ramus and marking the anterior attachment of the masseter lateralis, is not only very prominent as in most of the Hystricoidea, but shows a considerable lateral displacement at the point of divergence from the ramus. The reduction of the angular process itself is very possibly an adaptive feature, due to the saltigrade attitude of the animal and the consequent increase in the degree of flexion of the head.

The development of the infra-orbital foramen and of the zygo-masseteric structure is also more comparable to that of the Hystricomorpha than to the great majority of the other members of the Order. On the other hand the Pedetidae retain the primitive lacrymo-jugal contact which, according to Gregory (1920), is never retained in the Hystricomorpha. Moreover the structural significance of the lacrymal bone appears to be similar to that in the Sciuromorpha and in some of the Myomorpha. In both these features, however, the Pedetidae merely share a common primitive condition which occurs in many widely separated groups, and which does not necessarily imply any near relationship.

The significance of the extent of fusion between the tibia and fibula seems to be somewhat doubtful, except, perhaps, with regard to the " end-products " of evolutionary development, for it may be assumed that those species in which fusion is complete were derived from ancestors in which the two bones were distinct.

In the past there has been much speculation as to the ancestry and relationships of the Pedetidae. This is summarised by Simpson (1945) who records that they " have been placed in irreconcilably different systematic positions, and are really of quite unknown affinities ". Simpson himself places the family under the general heading " ? Anomaluroidea *incertae sedis* ", which in turn is placed under " ? Sciuromorpha *incertae sedis* ". As Ellerman (1940–49) points out, this brings *Pedetes* into the Sciuromorpha ; a classification which he finds " quite impossible to believe ".

There is undoubtedly no close relationship between the Pedetidae and any other known family, but from the study of *Megapedetes* there seems to be nothing to preclude the possibility of remote Hystricomorph connections. The fact remains, however, that as far as our knowledge goes at present, the Pedetidae are no more closely allied to any one rodent family than they are to several other families. Indeed Simpson's comment on the anomaluroids could as well be applied to the pedetids, that from the available evidence there is equally good reason for placing them " anywhere or nowhere, with respect to the classic subdivisions of rodents ".

In view of the fact that the known members of the family are at present restricted to a single living genus and two fossil genera, the systematic classification must necessarily remain in doubt until further evidence is forthcoming to throw new light upon their antecedents. It seems advisable therefore to follow Ellerman, who concludes that the Pedetidae should be regarded as a distinct superfamily. Ellerman's diagnosis of the characters of the superfamily is, of course, based upon those of the living genus, and although the new fossil genus agrees in most respects,

there are two important points of difference : (1) that the cheek-teeth are of limited growth, and (2) that there is no reduction in the number of digits in the hind foot.

In certain instances a difference in the number of digits, or in the structure and growth of the teeth may occur amongst members of a single family, but such variations are not normally to be found within any of the smaller sub-divisions of the mammalia. These features are therefore considered to be of sufficient importance to warrant the recognition of subfamily status for the Megapedetinae.

REFERENCES

DIETRICH, W. O. 1942. Ältestquartäre Säugetiere aus der südlichen Serengeti : Deutsch-Ostafrika. *Paläontographica*, Stuttgart, 94, A : 43-133, pls. 3-23.

ELLERMAN, J. R. 1940–49. *The Families and Genera of Living Rodents.* Brit. Mus. (Nat. Hist.), London. Vols. I–III(1).

GREGORY, W. K. 1920. Studies in Comparative Myology and Osteology : No. IV. A Review of the Evolution of the Lacrymal Bone of Vertebrates, with special reference to that of Mammals. *Bull. Amer. Mus. Nat. Hist.*, N.Y., **42** : 95-263, pl. 17.

SIMPSON, G. G. 1945. The Principles of Classification and a Classification of Mammals. *Bull. Amer. Mus. Nat. Hist.*, N.Y., **85** : 1-350.

STROMER, E. 1926. Reste Land– und Süsswasser-bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. *In* Kaiser, E. *Die Diamantenwüste Südwest-Afrikas*, 2 : 107-153, pls. 40-42.

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EXPLANATION OF PLATE

Megapedetes pentadactylus gen. et sp. nov.

FIG. 1. Skull and mandible of holotype : left lateral aspect . × 1.

FIG. 2. Left upper cheek-teeth of holotype : $Pm^4 - M^2$. ×3 approx.

FIG. 3. Left lower cheek-teeth of holotype : $Pm_4 - M_3$. ×3 approx.

FIG. 1

FIG. 2

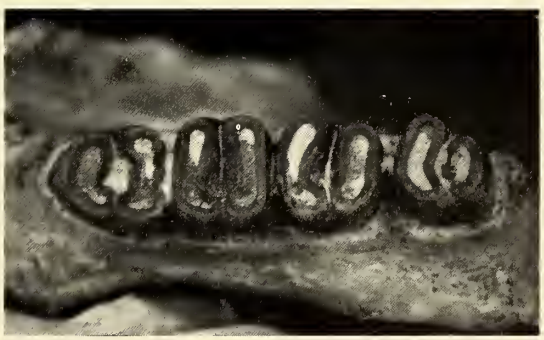

FIG 3

MEGAPEDETES